

OSTRACOD ASSEMBLAGES AND THE DEPOSITIONAL ENVIRONMENTS OF THE HEADON, OSBORNE, AND BEMBRIDGE BEDS (UPPER EOCENE) OF THE HAMPSHIRE BASIN

by M. C. KEEN

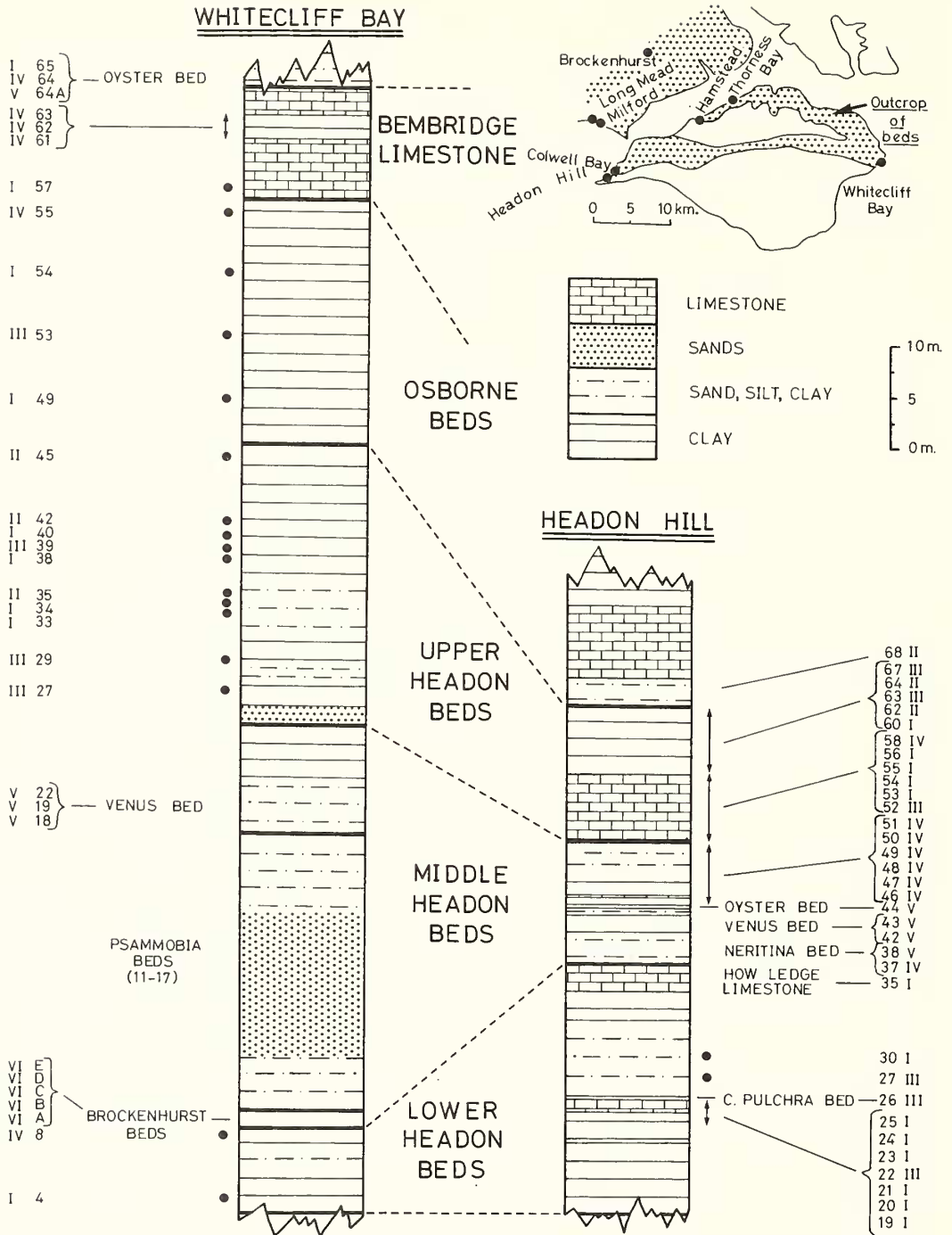
ABSTRACT. Six ostracod assemblages have been recognized from the Headon-Bembridge Beds of the Hampshire Basin by the use of cluster analysis employing Jaccard and Dice Coefficients. They are thought to be salinity controlled and are comparable with Recent ostracod assemblages. Two are believed to represent a freshwater environment (0–3‰ salinity), the first characterized by *Candona* and *Cypridopsis*, the second by *Moenocypris*. Three are believed to represent brackish environments, characterized by *Cytheromorpha* (3–9‰), *Neocyprideis* (9.0–16.5‰), and *Haplocytheridea* (16.5–35.0‰). The sixth assemblage is believed to represent a truly marine environment. Evidence for post-mortem movement of valves and for mixed assemblages is examined. The autecology of *N. colwellensis* (Jones) is studied, especially the relationship between salinity and size and the development of nodes; variation in carapace ornament is believed to be related to CaCO₃ content of the water. Seven new species and two new subspecies are described.

THE 'Tertiary Fluvio-marine Formation' of Hampshire and the Isle of Wight has attracted the attention of many geologists interested in ancient environments. Amongst the early workers the most outstanding was Edward Forbes, who recognized the freshwater, estuarine, and marine nature of the deposits in his classic work of 1856. In more recent years palaeoecological aspects have been investigated by Bhatia (1957) and Murray and Wright (1974) with Foraminifera; Daley (1972, 1973) on the molluscan assemblages of the Bembridge Beds; Edwards (1967) using the total fauna; and Haskins (1971*c*) and Keen (1972*a*) with ostracods.

The ostracods are particularly suited for an investigation of these deposits because of their wide environmental range. Recent years have seen a vast increase in ecological data on living ostracods, so there is now a firm foundation for palaeoecological studies. The taxonomy of these upper Eocene species is also in a reasonably healthy state due to the work of Jones (1856, 1857), Jones and Sherborn (1889), Haskins (1968*a*–1971*b*), and Keen (1972*a, b*, 1973*a, b*). Haskins (1971*c*) used ostracods to determine the depositional environments of the Palaeogene of the Isle of Wight, recognizing freshwater, brackish, and marine assemblages in the Headon-Bembridge Beds. Six assemblages are recognized herein, probably essentially salinity controlled. They are comparable with Recent ostracod assemblages, in particular with those recorded from lagoons bordering the Gulf of Mexico.

The horizons studied (text-fig. 1) are the Headon and Osborne Beds, Bembridge Limestone, Bembridge Oyster Bed, and Bembridge Marls. Sampling details for the two main sections, Headon Hill and Whitecliff Bay, are shown in text-fig. 1.

The age of the deposits remains controversial. The base of the Middle Headon Beds has traditionally been regarded by British palaeontologists as the base of the



TEXT-FIG. 1. Sections at Headon Hill and Whitecliff Bay, showing the positions of ostracod-bearing samples; arabic numerals indicate sample number, roman numerals the assemblage to which they belong.

Oligocene, so they have been placed into the Lattorfian, the basal Oligocene stage. Others have placed the boundary at a higher position, often drawing the base of the Oligocene at the base of the Hamstead Beds. This is the view adopted here, so the Headon-Bembridge Beds are regarded as being of late Eocene age. Edwards (1971) gives a full bibliography.

The area of sedimentation was probably a restricted basin bounded by the Portsdown uplift to the north and the Brixton-Sandown uplift to the south. An eastward-flowing river system emptied into this, with the open sea lying to the east and south-east. The sea sometimes penetrated the embayment, giving rise to lagoonal and marine conditions. Evidence of contemporary earth movements has been deduced by Daley and Edwards (1971).

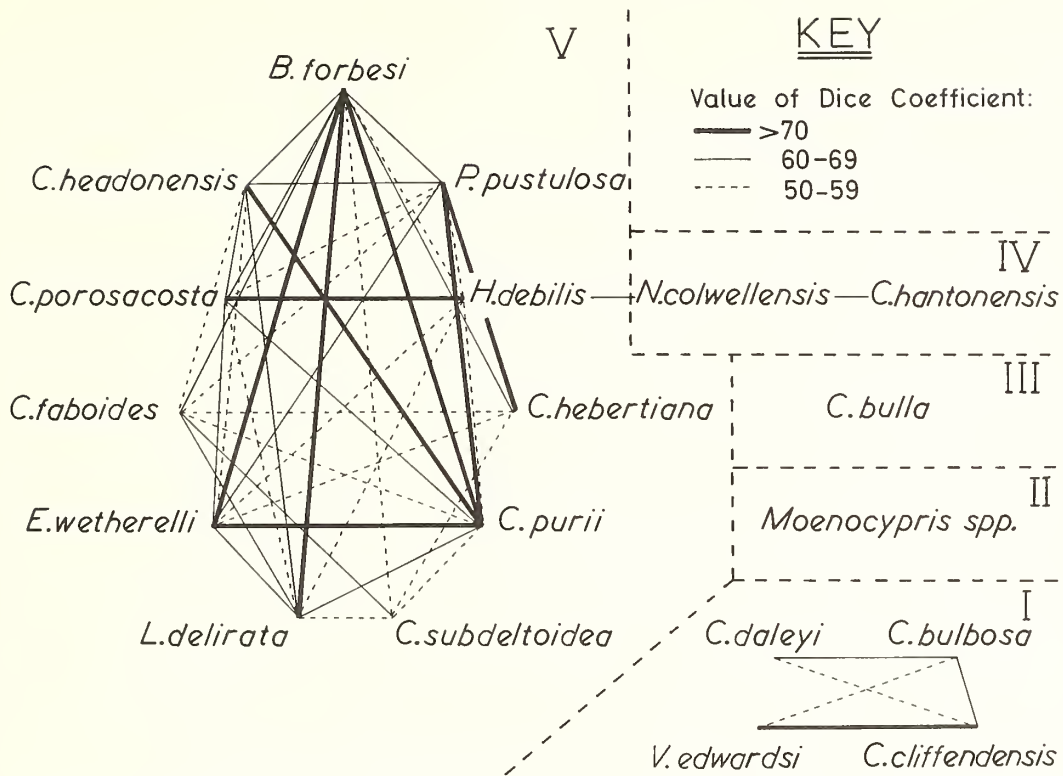
METHODS

One hundred and seventy-six samples were examined, of which ninety-one yielded ostracods. It had originally been decided to count the number of specimens of each species per unit volume of unwashed sediment, but this had to be abandoned as impractical. Some samples yielded several hundred specimens within a short period of time, while others needed several hours in order to find a dozen or so specimens. While it is possible to average out the number of specimens present to a standard unit volume, this practice was not followed because of the great discrepancies between the size of the final samples. The problem may not be too important, however, since the rate of sedimentation is unknown, and volume for volume comparisons may not have much significance; for example, does a high frequency of valves indicate slow deposition of sediment or dense populations? Secondly, the assemblages have been determined by using cluster analysis, which requires the recording of the presence or absence of a species in a particular sample. Thus the main consideration is whether a large enough sample has been examined to record all the species present. Kornicker (1965) has indicated that a sample of 300 specimens yields most species present, while even 150 approaches the actual number. These numbers were readily available for the mesohaline and polyhaline assemblages, but difficult to obtain for the freshwater ostracods, and so this criterion was waived for the latter. Table 1 shows the number of specimens examined in assemblages III, IV, and V.

Cluster analysis is now a fairly standard technique, and various correlation coefficients have been used for determining ostracod assemblages (Kaesler 1966; Carbonnel 1969; and Cheetham and Hazel 1969). The computer program used in this study is that given by Bonham-Carter (1967). Clustering is by the unweighted pair-group method. In the analysis of the data only the common species were considered, defined as those present in five or more samples, and representing at least 3% of the fauna in each sample; nineteen species fall into this category. The reason for eliminating the rare species is that their presence or absence in a sample is much more a matter of chance than for the common species. The results are presented in two forms. Text-fig. 2 is an R-mode analysis using the Dice Coefficient, presented as a constellation diagram, and using simple absence/presence data. The five assemblages are shown as being distinct more graphically than by using a dendrogram. The species of Assemblage V form a large and well-defined cluster with high

TABLE 1. Composition of samples belonging to Assemblages III, IV, and V. N = number of individuals; figures for genera indicate percentage occurrence. Note that, because only the common genera have been used, the percentages do not always total 100. Also note some anomalies that occur due to the clustering method; for example, WB8 with 67% *Neocyprideis* belongs to Assemblage III rather than IV, while BC5 with only 32% *Neocyprideis* belongs to Assemblage IV: this is because of the presence of a third genus, *Cladarocythere* in BC5. Note also the increase in diversity from Assemblage III, through IV, to Assemblage V.

SAMPLE	N	CYTHROMORPHA	NEOCYPRIDEIS	CLADAROCYHERE	HAPLOCYTHERIDEA	BRADLEYA	CLITHROCYPHERIDEA	CYAMOCYTHERIDEA	CYTHRETTA	EOCYTHEROPTERON	LEGUMINOCYTHEREIS	PTERYGOCYTHEREIS	ASSEMBLAGE
HH 22	112	50	50										III
HH 26	103	99	1										
WB 8	108	33	67										
WB 27	55	100											
WB 29	96	95	3										
WB 39	31	65	33										
WB 53	95	89	11										
HHCP 6	306	83	6										
HHCP 13	77	50											
HH 37	337	26	60	13	1								
HH 47	398		35	5	25								
HH 48	438	1	77	10	6								
HH 50	218		80	8									
HH 51	85		69	12									
HH 58	287		82	17									
CB 6	99	1	58	1	6	2	1	19	1	8	8	1	
BC 5	96	63	32	4									
BC 8	173		100										
WB 63	61	2	96		2								
WB 64	53	1	97		2								
NHH 1	183		56	22	22								
NHH 3	66	2	97										
HH 38	115	31			64	1				2		2	V
HH 42	200	2	10	1	55	8	7	4	4		1	2	
HH 43	348		8	1	29	3	16	10	16	1	4	6	
HH 44	403	2	4	1	62	3	1	16	8	2	1	1	
CB 1	111		2		39	3	2	5	30	2	10		
CB 2	86	1			54	1	1	15	8	6	3	2	
CB 4	813				57	6	1	24	3	2	2		
CB 5	147	1	1		70	1	1	21					
MF 1	242		7	1	11	7	7	15	48	1	3	1	
MF 2	173	1	5		13	10	3	10	53	1	3	1	
BR 3	113	5	5		29	2		1	40	5		8	
WB 18	160	4			55			1	25	5		1	
WB 19	175	14			54	3	1	1	13			7	
WB 22	120	1			40				10				
WB 64a	68	2	2		85								
Base VB	132	1	12	1	24	12	2	3	32	1	2	2	
Mid VB	91	1	5		31	15	9	6	25	1	1	2	
Top VB	549	1	6		31	9	4	5	34	1	3	1	

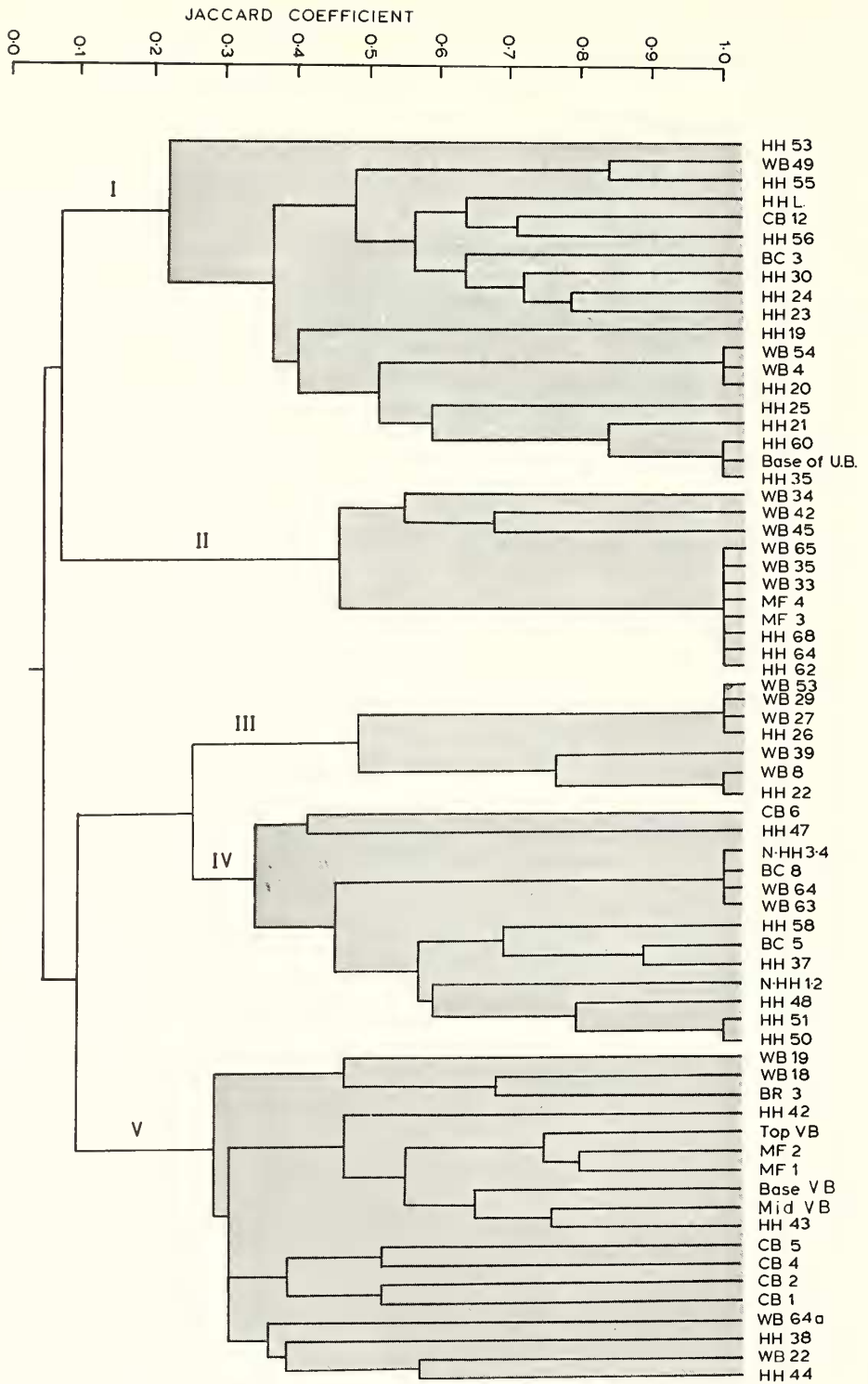


TEXT-FIG. 2. Constellation diagram showing the level of association between the nineteen common species. This is an R-mode analysis using the Dice Coefficient of correlation. Roman numerals indicate the five assemblages which can be recognized.

correlation values between one another, indicating that they frequently occur together. Only one species, *Haplocytheridea debilis*, has a significant correlation with a species belonging to another assemblage. Text-fig. 3 is a Q-mode analysis using the Jaccard Coefficient, presented as a dendrogram, but the species here are divided into absent (< 3%), present (3-25%), and abundant (> 25%) for analysis. In text-fig. 4 the assemblages are shown, together with rare species assigned to them, and with suggested salinities.

OSTRACOD ASSEMBLAGES

The assemblages recognized here are biofacies, i.e. groups of fossils frequently occurring together, and assumed to have had similar environmental requirements. The first part of the definition is supported by the statistical results, the second is deduced by comparison with living relatives. The environment is thought to be the primary control, interrelationships between organisms being secondary. The distribution of individual species differ, giving overlap between some of the assemblages. This is the case with modern marine communities, and is to be expected if



TEXT-FIG. 3. Dendrogram of Q-mode analysis using the Jaccard Coefficient of correlation. For locality details see Appendix.

the environmental needs of the species within a community are not exactly identical. In this study, overlap is particularly apparent with the brackish water assemblages, where there is almost complete gradation from one assemblage to another, while within assemblages some species are more widespread than others.

The trophic role of ostracods has never been studied in any detail, although they are known to be predominantly scavengers, with some herbivores. They do not seem to be the specific prey of any animals, apart perhaps from the young stages of some boring gastropods, being eaten by benthonic suspension feeders and nektonic filter feeders. Shelter is important for many ostracods, and this can be provided by vegetation or animals such as bryozoans; other ostracods live interstitially and so are independent even of this. Therefore it seems reasonable to consider the environment as the primary control, and the presence of other organisms as secondary. Comparison with living ostracods suggests that there was no interdependence between the ostracods themselves. Following from this, it appears justifiable to consider the ostracods on their own, without detailed consideration of the other phyla present.

Once the assemblages have been recognized, there are other problems to consider. Within any over-all environment there will be different microenvironments; as mentioned above, some ostracods would have lived interstitially, others crawled over the bottom sediment, some lived amongst the weed, others swam amongst it. On death, all of these will be found in the same sediment, giving a single assemblage. It is possible to recognize some of these life styles amongst the freshwater ostracods by comparison with living relatives (Keen 1975), but generally this is not so. However, even with Recent ostracods it is usually impossible to be more precise. Transportation after death is another factor to consider, and is discussed in more detail below. However, the assemblages are thought to represent the fossilized remnants of living communities, and as such, approach the ideal of a palaeontologically defined biocoenosis. This does not mean that no movement occurred after death, but it does imply that such movement was of a limited amount. Individual cases of mixed assemblages are discussed in the relevant sections below.

One final problem remains to be considered. As will be seen from the following discussion, many of the deposits are regarded as lagoonal. By comparison with modern lagoons, sedimentation would have been slow, but rapid changes in environmental conditions could be expected. It is therefore possible that the samples have mixed more than one environment since they were collected from a vertical thickness of about 6 cm. In order to test this idea, three horizons were resampled in detail. Firstly, a small thickness of sediment was sampled in the field using a trowel; a minimum thickness of 2-3 cm could be collected in this way. A second method was to use an aluminium tray, 60 cm long, 5 cm deep, and 10 cm wide which was pressed into a carefully trimmed section, and a spade used to cut it out. In this way a complete section 60 cm long remained in the tray. Top and bottom were marked on the tray, and then it was wrapped in polythene to retain the moisture of the sediment. The sample was examined in the laboratory. Using this method it was possible to examine 0.5-1.0 cm thicknesses of sediment. Thus, in addition to the 176 samples already mentioned, a further fifty-three samples were examined in detail. However, the latter were not used in the statistics because they were from selected horizons and would have heavily weighted the results: e.g. there would have been another thirty

samples of Assemblage V from only 50 cm of sediment, which is out of all proportion to sampling from other horizons. The results obtained from these additional samples are discussed further in the relevant sections below. The most important conclusion, however, is that the original samples are perfectly adequate for this study.

FRESHWATER OSTRACOD ASSEMBLAGES

Two distinct freshwater assemblages which can be recognized have been dealt with in greater detail by Keen (1975). Both can be recognized in the Hamstead Beds (Keen 1972a), and are also recorded from the Palaeogene of the Paris Basin, Rhine Valley, Mainz Basin, and Hesse.

Assemblage I. The *Candona-Cypridopsis* Assemblage. This is characterized by *Candona* spp. and *Cypridopsis* spp., with *Virgatocypris edwardsi* sp. nov. and *Cypria dorsalta* Malz and Moayedpour. Associated molluscs are *Galba* and *Planorbina*, with rare *Melanopsis*. *Chara* is usually abundant and seeds of waterplants often present. The sediment is a grey-green clay, a black carbonaceous clay, or a buff limestone. *V. edwardsi*, *Candona cliffendensis* sp. nov., and *Cypridopsis bulbosa* (Haskins) have a significant relationship with limestones; using a χ^2 test p was found to be 0.001, 0.005, and 0.03 respectively (Keen 1975). The first two species are more or less restricted to limestones, but *C. bulbosa* has a much wider distribution. Only one assemblage is recognized, although it could be divided into two sub-assemblages, i.e. one from limestones, and the other from clays.

Assemblage II. The *Moeno-cypris* Assemblage. *Moeno-cypris* is the only ostracod belonging here. Two species are present, *M. sherborni* Keen in the Lower Headon Beds, and its descendant *M. reidi* Keen in the Upper Headon and Osborne Beds. *Moeno-cypris* is an extinct genus, but there is little doubt that it inhabited freshwater (Keen 1975). The samples come from grey clays with common *Viviparus*, *Melanopsis*, and *Unio*, rarer *Potamaclis* (Fam. Melaniidae); serpulids (sometimes present); and *Chara* (rare). Seeds of waterplants are often abundant.

There is little doubt that these two assemblages inhabited freshwater. The difficulty is in accounting for the existence of two distinct assemblages. A certain amount of mixing is indicated by the coefficients of correlation; *Moeno-cypris-Cypridopsis bulbosa* is 17, with lesser values between other members of Assemblage I and *Moeno-cypris*. Such values can be explained by post-mortem movement. The controlling factor is believed to be the depth of water. Daley (1972) has already discussed this with regard to the molluscan assemblages, and Keen (1975) concerning the ostracods, so it is only necessary to give the conclusions here. The *Candona-Cypridopsis* Assemblage is thought to have characterized lake margins or shallow lakes up to about 1 m or so in depth. This would coincide with the upper infra littoral zone, or zone of emergent waterplants. The water would have been still or slowly moving, with an alkaline pH (~ 8) and a positive Eh. The *Moeno-cypris* Assemblage is thought to have characterized deeper water (2-15 m?) coinciding with the lower infra littoral zone, or zone of submerged waterplants, or bare muddy bottoms. The water would have been still, with poor circulation, an alkaline pH, and the bottom sediments probably had a negative Eh.

BRACKISH WATER ASSEMBLAGES

Three brackish water assemblages have been recognized, ranging from a low salinity assemblage, through mesohaline, to polyhaline.

Assemblage III. The *Cytheromorpha* Assemblage. This is characterized by *C. bulla* Haskins; other ostracods found here are discussed below. This assemblage is more common than indicated on the dendrogram, but several samples could not be included in the analysis because they contained too few specimens. It is found in two differing sediments: the first is a grey clay with abundant shells of the bivalve *Potamomya plana* J. Sowerby, subordinate *Melanopsis*, *Theodoxus*, and *Corbicula*, with rare *Viviparus*, *Galba*, and *Planorbina*; the second is a green clay with few or no molluscs. *Cytheromorpha* is found at the present day in salinities ranging from 0–35‰. It is characteristic of brackish waters. Wagner (1957) records it from lower mesohaline (2–10‰); Puri (1968) from an estuarine environment (0–26‰); Swain (1955) from typical Texan bays (2–10‰); Curtis (1960) as being typical of 'closed shallow lagoons, away from fluvial influence and with little marine influence'. The living molluscs are typical of subtropical rivers and estuaries. The presence of rare *Galba*, *Planorbina*, and *Viviparus* suggest a fluvial influence, although these shells are probably allochthonous. It is usually assumed that the poorest brackish water assemblages, in terms of number of species, are found in salinities below 9‰. This assemblage has the least number of species, and, together with the known range of living *Cytheromorpha*, is taken to indicate a salinity of 3–9‰.

Assemblage IV. The *Neocyprideis* Assemblage. *N. colwellensis* (Jones) is the dominant ostracod of this assemblage, although the actual composition varies between samples. *Cladarocythere* spp. are commonly present, *Cytheromorpha bulla* and *Haplocytheridea debilis* (Jones) more rarely. *Bradleya favosa* Haskins is assigned to this assemblage, although as it only occurs four times it was not considered statistically; it is only found in samples dominated by *N. colwellensis*. It is placed in *Bradleya* for convenience, belonging to an undescribed genus; a second species, *B. dolabra* Keen has been described from Oligocene brackish water deposits (Keen 1972a). The sediment is a clay or sandy clay. The molluscan fauna varies; samples with *C. bulla* contain juvenile *Galba*, *Planorbina*, and *Corbicula obovata* (J. Sowerby); a distinctive fauna from the Middle Headon Beds consists of *Batillaria ventricosa* (J. Sowerby), *Potamides vagus* (Solander), *Globularia grosa* (Deshayes), and rare *Ostrea*: *B. favosa* and *H. debilis* are found with this second association. The commonest molluscs, however, are *C. obovata* and *P. vagus*. The Foraminifera *Quinqueloculina* is sometimes present.

Neocyprideis is an extinct genus, but is closely related to the living *Cyprideis*, which some believe to be its descendant. The latter is probably the most typical brackish water ostracod; its ecology has been fully described by Sandberg (1964): it is found in freshwater, is common in mesohaline waters, rarer in polyhaline and euhaline waters, but abundant in hypersaline conditions. Its greatest development is in mesohaline salinities. It usually inhabits relatively quiet water, such as creeks bordering estuaries, lagoons, or brackish 'ponds' close to the sea (Whittaker, pers. comm. 1975). It is a bottom crawler, or burrower, feeding on organic matter in the

sediment. In low salinities, *Cyprideis* develops nodes on its shell, and may increase in size; these factors are studied below. Assemblage IV is taken to represent salinities of 9·0–16·5‰. The other characteristic ostracod of this assemblage is *Cladarocythere hantonensis*. This extinct genus is found in Eocene and Oligocene brackish water sediments. Its ecology can only be derived from associated faunal elements, and there is some indication that different species had differing salinity preferences. *C. hantonensis* is taken to have inhabited upper mesohaline and polyhaline salinities, but *C. apostolescui* (Margerie) has been taken to belong to lower mesohaline salinities in the Paris Basin (Keen 1971, 1972a). This species is also present in the Hampshire Basin and represents a special assemblage consisting almost entirely of *C. apostolescui*. It is found in the marl immediately below the topmost Bembridge Limestone at Whitecliff Bay, Thorness Bay, and Bouldnor Cliff. Because it occurred in only four samples it could not be included in the cluster analysis, neither could the samples containing it, because the only other ostracod present, *Neocyprideis*, represented less than 3% of the fauna and so counted as 'absent' under the procedure adopted for this study.

Assemblage V. The *Haplocytheridea* Assemblage. This is characterized by *H. debilis*. The sediment is a silty or sandy clay, often with large numbers of *C. obovata* in life positions. Other molluscs include *Sinodia suborbicularis* (Goldfuss), *Ostrea*, *Globularia*, *Nucula*, *Natica*, and a few *Galba* and *Planorbina*. The Foraminifera *Rotalia* and *Quinqueloculina* are commonly present.

Living *Haplocytheridea* are recorded from estuarine and open lagoonal environments, especially along the coast of Texas, Louisiana, and Florida. They are recorded from: depths up to 21 ft, salinity 16–33‰ (Curtis 1960); the Lower Bay subfacies, salinity 10–17‰ (Swain 1955); rocky tide pools of normal marine salinity (Benson *in* Moore 1961); mangrove swamps and marine environment, salinity 23–40‰ (Benda and Puri 1962); shallow marine waters (Hulings and Puri 1964); lagoonal areas, salinity 10–25‰ (Engel and Swain 1967). Howe (1971) has shown how torose cytherideidae, which includes *Haplocytheridea*, have been used by petroleum geologists to locate ancient shorelines in the Gulf states of America; thus *Haplocytheridea* is regarded as being typical of areas adjacent to the shoreline, usually lagoonal or estuarine, and generally indicating reduced salinities. From this it can be seen that *Haplocytheridea* is typical of polyhaline and marine salinities. The other ostracods present vary from sample to sample, but those with living relatives, i.e. *Cuslmanidea*, *Cytheretta*, *Cytherella*, *Paijenborchella*, *Paracytheridea*, *Pterygocythereis*, *Pontocythere*, and *Krithe*, are essentially marine genera, although most can adapt to polyhaline conditions (Swain 1955; Curtis 1960; and especially Puri 1968). Assemblage V is taken to indicate a polyhaline environment, salinity ranging from 16·5 to 35·0‰. The differences between samples is discussed further below. The possibility of hypersaline conditions must be borne in mind. These would have been very temporary, and due to evaporation. There is no geological evidence for permanent high salinities; there are no evaporites, and there is ample evidence of freshwater conditions with many water plants, and lowland vegetation. This contrasts with conditions in the Paris Basin.

THE BROCKENHURST BED

Assemblage VI. The Hazelina Assemblage. There were not enough samples from this thin (50–100 cm) horizon to warrant statistical treatment. However, the characteristic fauna suggests that this could be regarded as a separate assemblage. It lacks many of the characteristic polyhaline species of Assemblage V, while the presence of such genera as *Bairdia*, *Hazelina*, and *Idiocythere* suggest truly marine conditions. Molluscs are *Natica*, *Ostrea*, *Modiola*, *Cardium*, *Fusus*, and *Voluta*; solitary corals are recorded; Foraminifera are *Cibicides*, *Rotalia*, *Globigerina*, and *Nonion*.

The paucity of the fauna suggests near-shore, perhaps even sublittoral waters, but of normal marine salinity.

MARSH FACIES

Finally, there is a widespread facies which has not yielded ostracods. It consists of finely laminated clay and sand, sometimes with thin lignitic layers. It is considered to represent a marsh facies. It is especially prominent in the Lower and Upper Headon Beds.

LIFE AND DEATH ASSEMBLAGES

It has been suggested that Assemblages III, IV, and V are salinity controlled and probably formed a gradational sequence. Species which had a broad environmental tolerance probably lived amongst more than one assemblage, while movement of valves after death could lead to mixing of assemblages. *Cytheromorpha bulla*, *Neocyprideis colwellensis*, and *Haplocytheridea debilis* are commonly present in more than one assemblage, so it is worth considering in some detail whether their distribution is due to post-mortem movement or reflects original life habitats. Living members of these genera, as noted above, are adapted to a wide range of salinities, so it is possible that these fossil species might have behaved similarly.

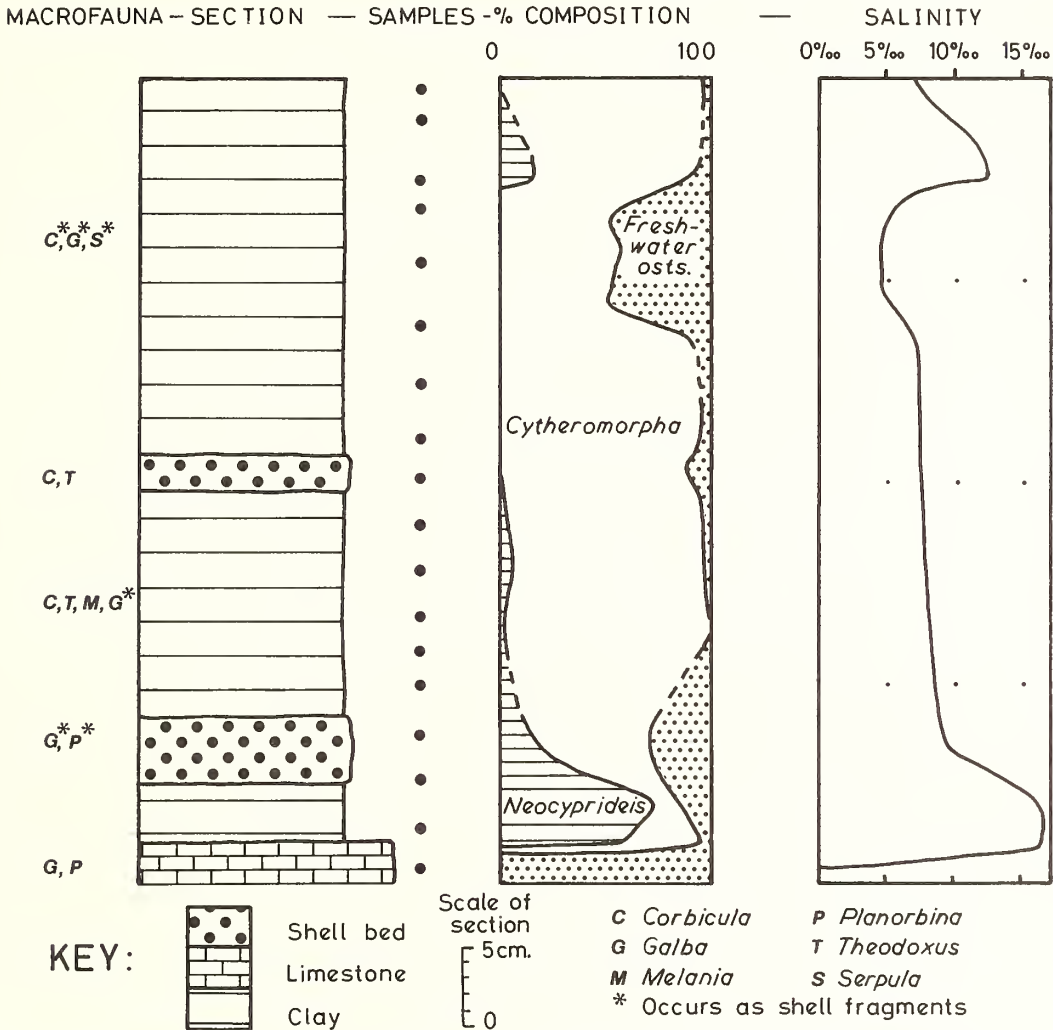
Several criteria have been used to indicate an ostracod biocoenosis: presence of several different moult stages, including adults; presence of carapaces rather than single valves; and equal numbers of each valve. The following example illustrates the use of these, together with stratigraphical succession and faunal composition. In text-fig. 5 a detailed section through the *Cyrena pulchra* Bed (Lower Headon Beds) is shown, with the percentages of *Neocyprideis*, *Cytheromorpha*, and freshwater ostracods from the various samples recorded, and a suggested salinity profile. The section starts in a buff limestone with numerous and well-preserved *Galba* and *Planorbina*. The ostracods belong to Assemblage I, contain many moult stages and adults, few specimens are broken, *Cypridopsis* in particular has many carapaces, and there are approximately equal numbers of each valve of each moult stage. This indicates little post-mortem movement, and so is taken to represent the biocoenosis. Immediately above the limestone, the green clay contains many small fragments of *Galba*; the most abundant ostracod is *Neocyprideis*, with common *Cytheromorpha*, but very rare freshwater ostracods; the second sample is similar. Both of these

SPECIES SUGGESTED SALINITY ‰ →	ASSEMBLAGE					
	I	II	III	IV	V	VI
	0-3		3-9	9-16.5	16.5 - 25 - 33	33
<i>Condona cliffendensis</i> SP. NOV. <i>Cypridopsis hessani hantonensis</i> SUBSP. NOV. <i>Cyprio dorsalto</i> MALZ & MOAYEDPOUR <i>Cypris</i> sp. <i>Dorwinula</i> sp.	-----					
<i>Condona</i> sp. <i>Strandesio</i> cf. <i>spinosa</i> STCHEPINSKY ⁶ <i>Virgotocypris edwardsi</i> SP. NOV. <i>Virgotocypris</i> sp. ⁶ <i>Condona daleyi</i> SP. NOV.	-----					
<i>Cypridopsis bulbosa</i> (HASKINS) <i>Maenocypris sherborni</i> KEEN ¹ <i>Maenocypris reidi</i> KEEN ² <i>Cytheromorpha bullo</i> HASKINS ³ <i>Cytheromorpha unisulcata</i> (JONES) ⁴	-----	-----	-----			
<i>Cytherura pulchra</i> SP. NOV. <i>Neocyprideis colwellensis</i> (JONES) ⁵ <i>Neocyprideis williamsoniana</i> (BOSQUET) ⁶ <i>Cladocythere hantonensis</i> KEEN ⁶ <i>Cladocythere apostolescui</i> (MARGARIE) ⁶			-----	-----	-----	
<i>Bradleya favosa</i> HASKINS <i>Paracypris</i> sp. A. <i>Haplocytherideo debilis</i> (JONES) <i>Clithrocytherideo faboides</i> (BOSQUET) <i>Cushmanideo haskinsi</i> SP. NOV.			-----	-----	-----	
<i>Cushmanideo stinoni</i> SP. NOV. <i>Cushmanideo wightensis</i> SP. NOV. <i>Cyamocytherideo herbertiano</i> (BOSQUET) <i>Cyamocytherideo purii</i> HASKINS <i>Cyamocytherideo subdeltoida</i> HASKINS				-----	-----	
<i>Bradleya forbesi</i> (JONES & SHERBORN) <i>Cytherella pustulosa</i> KEIJ <i>Cythereilloideo lacunosa</i> HASKINS <i>Cytheretta heodonensis</i> HASKINS <i>Cytheretta porosocosta</i> KEEN				-----	-----	-----
<i>Eocytheropteron wetherelli</i> (JONES) <i>Flexus ludensis</i> KEEN <i>Leguminocythereis cancellosa</i> HASKINS <i>Leguminocythereis delirata</i> (JONES & SHERBORN) <i>Loxoconcha</i> sp.				-----	-----	-----
<i>Parocytheridea gradata</i> (BOSQUET) <i>Pajjenborchella brevicosta</i> HASKINS <i>Pterygocythereis pustulosa</i> HASKINS <i>Schulerideo perforata heodonensis</i> SUBSP. NOV. <i>Cytheretta</i> aff. <i>C. stigmoso</i> TRIEBEL				-----	-----	-----
<i>Haplocytheridea montelli</i> KEEN <i>Leguminocythereis</i> cf. <i>L. striatopunctata</i> (ROEMER) <i>Pokornyello osnabrugensis</i> (LIENENK LAUS) <i>Ruggeria semireticulata</i> HASKINS <i>Krithe bortonensis</i> (JONES)				-----	-----	-----
<i>Boirdio</i> sp. <i>Cythereello</i> cf. <i>C. compresso</i> (VON MUNSTER) <i>Cythereella</i> sp. <i>Hazelino indigeno</i> MOOS <i>? Idiocythere bortoniana</i> HASKINS <i>Pterygocythereis</i> cf. <i>P. fimbriata</i> (VON MUNSTER)					-----	-----

1 Lower Heaton Beds only	-----	Always present, usually abundant
2 Upper Heaton & Osborne Beds	-----	Usually present
3 Heaton Beds	-----	
4 Osborne & Bembridge Beds	-----	Rare
5 Heaton & Osborne Beds	-----	
6 Bembridge Beds	-----	Present as thanatocoenosis.

TEXT-FIG. 4. Ostracod assemblages from the Heaton-Bembridge Beds, with suggested salinities.

ostracods are represented by several different moult stages and contain similar numbers of each valve; these therefore represent the biocoenosis. The freshwater ostracods and molluscs are probably derived. Ascending the succession, *Neocyprideis* declines in numbers and eventually disappears, while *Cytheromorpha*



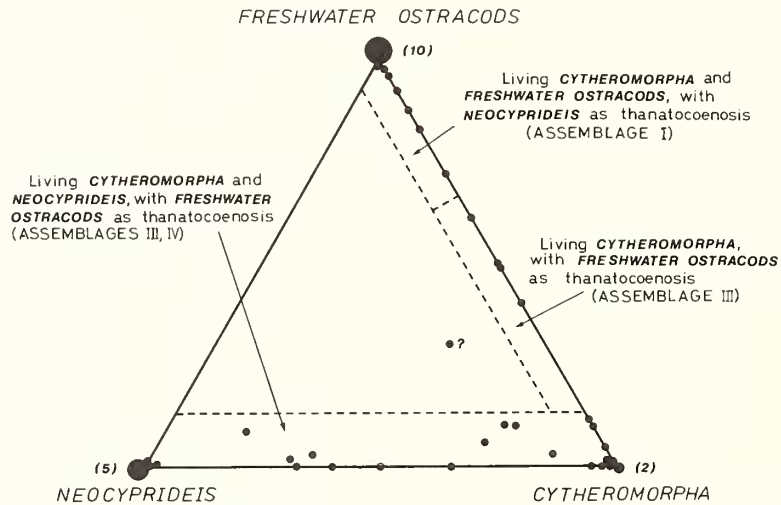
TEXT-FIG. 5. Section through the *Cyrena pulchra* Bed of Headon Hill, showing composition of ostracod fauna and suggested salinity.

becomes dominant. Towards the top the freshwater ostracods become common, forming up to 50% of the samples, but they are mainly represented by broken valves, with very few adults, while the freshwater molluscs are also fragmentary. They therefore represent fluviually transported material and belong to the thanatocoenosis. The section is interpreted as showing a shallow freshwater lake (Assemblage I)

situated near a coastline; the sea breached a barrier some distance away, leading to a rapid rise in salinity as the lake became converted into a lagoon. This caused the death of the freshwater animals and the introduction of a mesohaline fauna (Assemblage IV). The sea connection was short lived, the lagoon began to silt up, and freshwater influence increased (Assemblage III). Towards the top of the section fluvial influence was strong, introducing transported shells into the lagoon. Near the top, the reappearance of *Neocyprideis* and disappearance of the freshwater ostracods indicates another invasion of the sea, although this was not very long lived and the salinity was soon reduced.

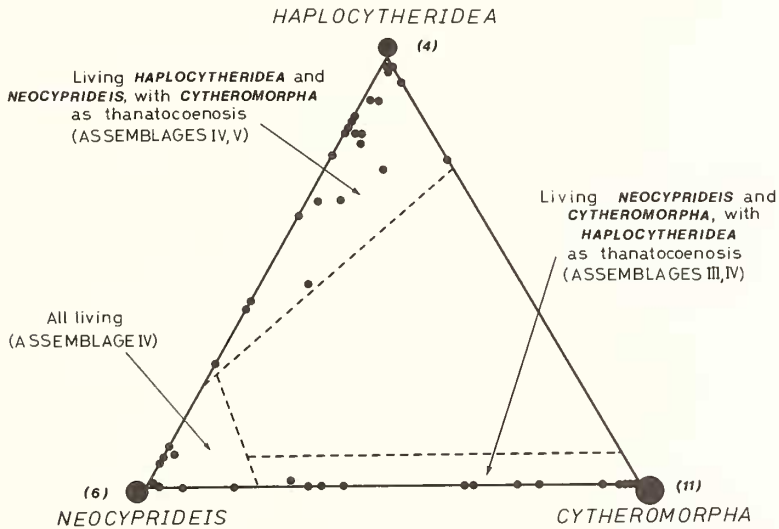
Another method of studying the samples is to regard them in terms of 'end-members' of gradational series. Four ostracod groups can be thought of as 'end members', *Haplocytheridea*, *Neocyprideis*, *Cytheromorpha*, and freshwater ostracods, so that each sample can be described in terms of the percentage occurrence of each of these. *Haplocytheridea* and the freshwater ostracods are almost mutually exclusive so we are left with a series of one, two, or three component samples which can be studied visually by using triangular diagrams. These are given in text-figs. 6 and 7. The first thing to notice, as would be expected, is that the samples do not plot in a random fashion, i.e. there is no scatter of points all over the diagram. Secondly, the samples show a continuous gradation from freshwater → *Cytheromorpha* → *Neocyprideis* → *Haplocytheridea* much as would be expected if the assemblages were controlled by a gradually changing parameter, in this case thought to be salinity.

The species present in each sample have been examined, using the criteria outlined above, to determine whether they were more probably biocoenosis or thanatocoenosis. It is admitted that the conclusions are relatively subjective, but when plotted on the diagrams they help in giving a consistent interpretation. In text-fig. 6 *C. bulla*, *N. colwellensis*, and freshwater ostracods have been plotted from fifty-one samples



TEXT-FIG. 6. Triangular diagram of samples belonging to Assemblages I-IV showing percentage composition of freshwater ostracods, *Cytheromorpha* and *Neocyprideis*.

excluding samples belonging to Assemblage V. It can be seen that *Neocyprideis* is rarely found in samples dominated by freshwater ostracods: in fact it only occurs once, and then forms only 1% of the fauna; these probably represent valves washed into a freshwater environment. On the other hand, freshwater ostracods are found in many samples dominated by *Cytheromorpha* and/or *Neocyprideis*; these are interpreted as valves carried by rivers into a lagoonal environment. The plots suggest complete gradation along the *Cytheromorpha*-freshwater and *Cytheromorpha*-*Neocyprideis* axes, indicating considerable overlap between living populations of these two sets of ostracods. In the case of *Cytheromorpha* and *Neocyprideis*, the presence of moults and adults, and equal numbers of each valve support this view. In the case of *Cytheromorpha* and the freshwater ostracods the same criteria suggest that *Cytheromorpha* could adapt to virtually freshwater conditions, occasionally forming a minor part of the freshwater biocoenosis; the freshwater ostracods in samples dominated by *Cytheromorpha* seem to belong to the thanatocoenosis.



TEXT-FIG. 7. Triangular diagram of samples belonging to Assemblages III-V showing percentage composition of *Haplocytheridea*, *Neocyprideis*, and *Cytheromorpha*.

In text-fig. 7 similar methods have been used to define the three fields indicated on the diagram. Thus *Cytheromorpha* is regarded as belonging to the thanatocoenosis in samples belonging to Assemblage V. These may represent dead valves carried by currents, or possibly stray animals which endured the increase in salinity, but could not breed. *Neocyprideis* is regarded as a living, breeding, member of the more brackish parts of Assemblage V.

One problem which could distort all of the above conclusions is that of rapidly changing conditions leading to *remanié* contamination. Thus, *Neocyprideis* might be inhabiting a mesohaline lagoon; a rapid rise in salinity could kill it and introduce a polyhaline fauna. With very slow sedimentation these two populations would become mixed. The example of the *Cyrena pulchra* Bed given above shows that

changing conditions can be recognized, at least in some cases, by detailed sampling. The case of *Neocyprideis* in Assemblage V needs some examination because it is often one of the most abundant constituents in samples from Headon Hill and Colwell Bay. With this in mind, the top 60 cm of the Venus Bed at Headon Hill were examined by taking thirty-three samples covering varying thicknesses of between 1 and 3 cm. The lowest 9 cm consisted of green clay, apparently without macrofossils, but containing fairly numerous *Candona*, represented by several different moult stages, some *Cypridopsis* and a few *Virgatocypris*, i.e. Assemblage I. The clay was extensively cut by burrows filled with the overlying sediment, so great care had to be taken to avoid contamination of samples. The overlying bed was a sandy clay, grading upwards into a fine sand, but extremely fossiliferous throughout. The burrows into the freshwater clay indicate that the clay was quite hard before burrowing took place, while the lack of burrows in the overlying sand could be taken as evidence of fairly rapid sedimentation. The burrow infills and the lowest 2 cm of this bed contained ostracods of Assemblage V together with freshwater ostracods, which, because of their preservation, were obviously derived from the underlying clay. The remaining 49 cm contained ostracods of Assemblage V, with *Neocyprideis* evenly distributed throughout. No unusual concentrations of the latter were found, as might be expected if it had only lived at certain times during this interval, and it was always represented by several different moult stages. It could be argued that the changes were so frequent as to destroy any horizons rich in *Neocyprideis*. Against this is the fact that layering of shells is present in the deposits, although bedding is poorly developed.

Secondly, we can consider the likely biology of *Neocyprideis*. If it was similar to *Cyprideis*, it probably had a single breeding season per year. Some support for this is indicated by the moult stages forming discrete groupings (text-fig. 11); ostracods which breed more than once a year do not often show this because those hatched during a warmer period grow faster, but are smaller, giving an almost continuous variation in size. If this was the case, *Neocyprideis* would have needed at least two to three years to establish the viable population indicated by the fossils. It also follows that its presence cannot be explained by seasonal fluctuations, i.e. *Neocyprideis* living at a time of the year when the salinity was lower. Migration may have been involved but seems unlikely by comparison with living *Cyprideis*. The evidence therefore suggests that *Neocyprideis* was a member of Assemblage V.

There is considerable variation between samples belonging to Assemblage V. Certain features are recognizable, however. Nearly all the samples are dominated by *H. debilis*, and *Cytheretta porosacosta* is usually next in abundance. There are notable differences between samples from Whitecliff Bay and those from the west of the Isle of Wight; *Clithrocytheridea*, *Cyamocytheridea*, and *Schuleridea* are rare in the east, but abundant in the west, while *Neocyprideis* is absent in the east. These genera are rather brackish water ones compared with the faunas found in the east. The differences between samples are probably due to differing salinities within the polyhaline range.

MORPHOLOGICAL VARIATION OF *NEOCYPRIDEIS COLWELLENSIS*

Brackish water ostracods show considerable variation in size and ornamentation related to variation in salinity. *N. colwellensis* was examined to see whether such variation offered any help in interpretation of environmental conditions. The results are given in Table 2.

TABLE 2. Distribution of size and nodosity in *Neocyprideis colwellensis* (Jones). Numbers in brackets are the number of measured female left valves; these numbers are low because adults normally form only about 10% of the preserved population. For discussion see text; for locality details see Appendix.

SAMPLE	NUMBER OF SPECIMENS	MEAN LENGTH ♀ L	ASSEMBLAGE	NODOSITY
WB 63 HH 58 CB 1 BR 1 VB 18 HHCP 2 NHH 4	58 (2) 240 (5) 2 (2) 6 (1) 5 (5) 104 (12) 66 (5)	.87 .85 .84 .84 .80 .78 .75	IV IV V V V IV IV	ADULTS AND INSTARS SMOOTH
HH 44 HH 42 HH 22 MF 1 NHH 3	16 (3) 20 (1) 56 (3) 17 (2) 65 (3)	.89 .87 .85 .84 .77	V V IV V IV	ADULTS SMOOTH, OCCASIONAL NODOSE INSTARS
HH 51 NHH 2 HH 47 NHH 1 HH 48	57 (5) 64 (2) 140 (10) 101 (11) 337 (21)	.80 .80 .79 .79 .76	IV IV IV IV IV	OCCASIONAL NODOSE ADULTS, MOST INSTARS NODOSE
HH 37	202 (13)	.77	IV	ALL COMMONLY NODOSE

Noding

Cyprideis and related genera develop hollow nodes or tubercles as a response to decreasing salinities. A salinity of 5‰ is often quoted as the figure below which noded forms become dominant. Vesper (1972a) has confirmed this in a detailed study of *C. torosa* (Jones); he found occasional noded adults in salinities up to 14‰, but between 6‰ and 2‰ they dramatically increased to form 85% of the population. The nodes are genetically controlled because they develop in specific places; Kilenyi (1972) believes that selection operates in favour of noded forms as the salinity decreases, eventually giving balanced polymorphism. With regard to *N. colwellensis*, only one sample (HH37) contains a high proportion of noded adults; this sample is intermediate between Assemblages III and IV. Noded adults are rare or absent in all other samples, although some samples of Assemblage IV have

common noded juveniles. Thus, if *N. colwellensis* reacted to decreasing salinity in the same way as *C. torosa*, it was never found in salinities below 5‰, lending support to the salinity suggested for Assemblage IV.

Size

There is some controversy over the relationship between size and salinity in ostracods; a recent review can be found in Van Harten (1975). Barker (1963) indicated a decrease in size with decreasing salinity in the ostracods *Leptocythere* and *Lox-concha*. These were marine forms adapting to an estuarine environment; with euryhaline species Hartmann (in Keen 1971) stated that size is independent of salinity. Vesper (1972b) appeared to confirm this in a study of *C. torosa*, suggesting a positive relationship between size and food supply. However, Van Harten (1975) found a significant negative correlation between size and salinity in this species, but the change was not gradual because populations from salinities below 5‰ were markedly larger than those from above. In this respect the increase in size appears to behave similarly to the increase in nodosity. *N. colwellensis* shows no clear relationship between size and suggested salinity. In general, specimens from Assemblage V fall into the upper part of the size range while those from Assemblage IV occur throughout the range. This, as with nodding, may be because *N. colwellensis* never inhabited salinities below 5‰, in which case the variation in size may be positively related to food supply.

Haskins (1969) observed that the largest specimens came from a sample collected immediately above the Bembridge Limestone, and postulated that this may have been related to an abundance of calcium carbonate in the water. Applying this to the present study this hypothesis seems unlikely. The largest specimens do come from lime-rich sediments, but so do relatively small ones; and the only pure limestone (HH58) yields individuals of about average size. Finally, although perhaps not strictly relevant to a brackish water animal, Reymont and Brannstrom (1963) found that in laboratory studies of the freshwater ostracod *Cypridopsis* those reared in abnormally high lime-rich waters or stagnant waters grew to a smaller size than those from the normal environment.

Variation in ornamentation

Specimens of *N. colwellensis* may be smooth or punctate. Five samples contained smooth forms, all coming from calcareous horizons. It is postulated that smooth forms are phenotypes which developed in lime-rich waters.

LIVING CONDITIONS OF THE BRACKISH WATER ASSEMBLAGES

The salinities indicated above are found in both estuarine and lagoonal areas and it is often difficult to differentiate between these in the geological record. Estuaries are high-energy environments with a great deal of transportation of material both from the sea and from the river, which leads to mixing of faunas. Freshwater faunas give way to brackish, which in turn give way to marine faunas; freshwater shells may be found throughout. This, in fact, has been found to be the case in the Headon Beds. Lagoons and bays have a more restricted access to the sea and are generally

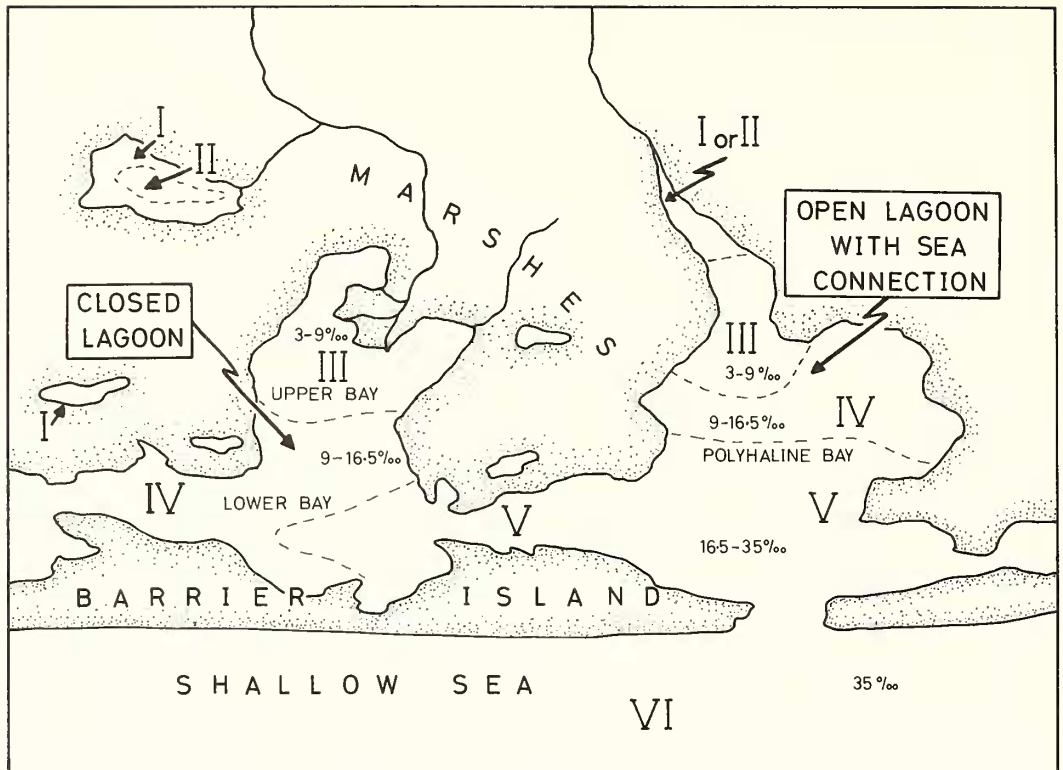
bodies of very shallow water with gradual salinity changes between lagoons. The fauna may give some indication as to which of these conditions prevailed. In the polyhaline part of modern estuaries the marine element is often represented by large numbers of species, but with few specimens of each, although it is impossible to generalize because much depends upon the size of the estuary (e.g. Wagner 1957; Kilenyi 1969; Whatley and Kaye 1971). Another imponderable is the tidal range, which affects the amount of transportation from the sea, and is itself determined by the palaeogeography. The polyhaline fauna of bays and lagoons is more restricted in numbers of species, many of which have their main habitat in the lagoons, and in that sense can be regarded as being more specialized than estuarine faunas. The fauna of the Headon Beds appears more similar to a lagoonal fauna than an estuarine one. Estuaries may, of course, enter into lagoons before reaching the sea, and many coastlines are a complex mixture of bays, lagoons, and estuaries. The procedure adopted is to look for a model in the present world, the most suitable being the complex system of bays and lagoons developed along the Texan coast.

These have been more intensively studied than other similar coastlines. The Hampshire Basin in late Eocene times exhibited features similar to those of Texas. Ladd *et al.* (1957) considered that the best classification of the lagoons was based on salinity, giving closed bays (0–20‰) and polyhaline bays (> 16.5‰). The latter are ‘front bays’ directly connected with the Gulf of Mexico by openings between sandy barrier islands, while the closed bays have no direct connection. Coastal streams drain into the lagoons, and salinity changes are gradual between the various bays. Short-term fluctuations occur: due to periods of drought, giving higher salinities; periods of high rainfall and floods, giving lower salinities; and periods of hurricanes and storms, when the sea may be swept into the lagoons. These rapid changes lead to the mass mortality of many of the animals inhabiting the waters of the lagoons. The lagoons are very shallow, mostly less than 9 ft deep. Studies in Florida show similar features; at Cape Romano (Benda and Puri 1962) a barrier of mangrove islands separates lagoons from the open sea. The lagoons are about 4 ft deep, with a salinity of 13–43‰; the mangrove swamps have numerous shallow baylets and inlets, with a salinity of 23–40‰.

Ostracod assemblages from these areas have been studied by Swain (1955; San Antonio Bay, a closed lagoon, Texas); Curtis (1960; Mississippi Delta); Benda and Puri (1962; Cape Romano, Florida); Hulings and Puri (1964; Florida); Engel and Swain (1967; Texas Gulf coast).

Assemblages III and IV are characteristic of the typical Bay Facies of Swain and the ‘closed shallow lagoon, away from fluvial influence and with little marine influence’ of Curtis. For reasons already given, Assemblage III is believed to represent a lower mesohaline environment (3–9‰) and Assemblage IV higher mesohaline (9.0–16.5‰). These would then correspond to the Upper Bay and Mid Bay subfacies respectively of Swain. Assemblage V corresponds well with the Lower Bay subfacies of Swain and the ‘open lagoon, small fluvial influence; marine influence prominent’ of Curtis. This is the polyhaline facies of Ladd *et al.*, where the lagoon has a connection with the open sea.

The environment envisaged for these deposits, therefore, is a series of lagoons, some open, i.e. with a direct sea connection, others closed, i.e. no direct connection



TEXT-FIG. 8. Suggested environments of the ostracod assemblages.

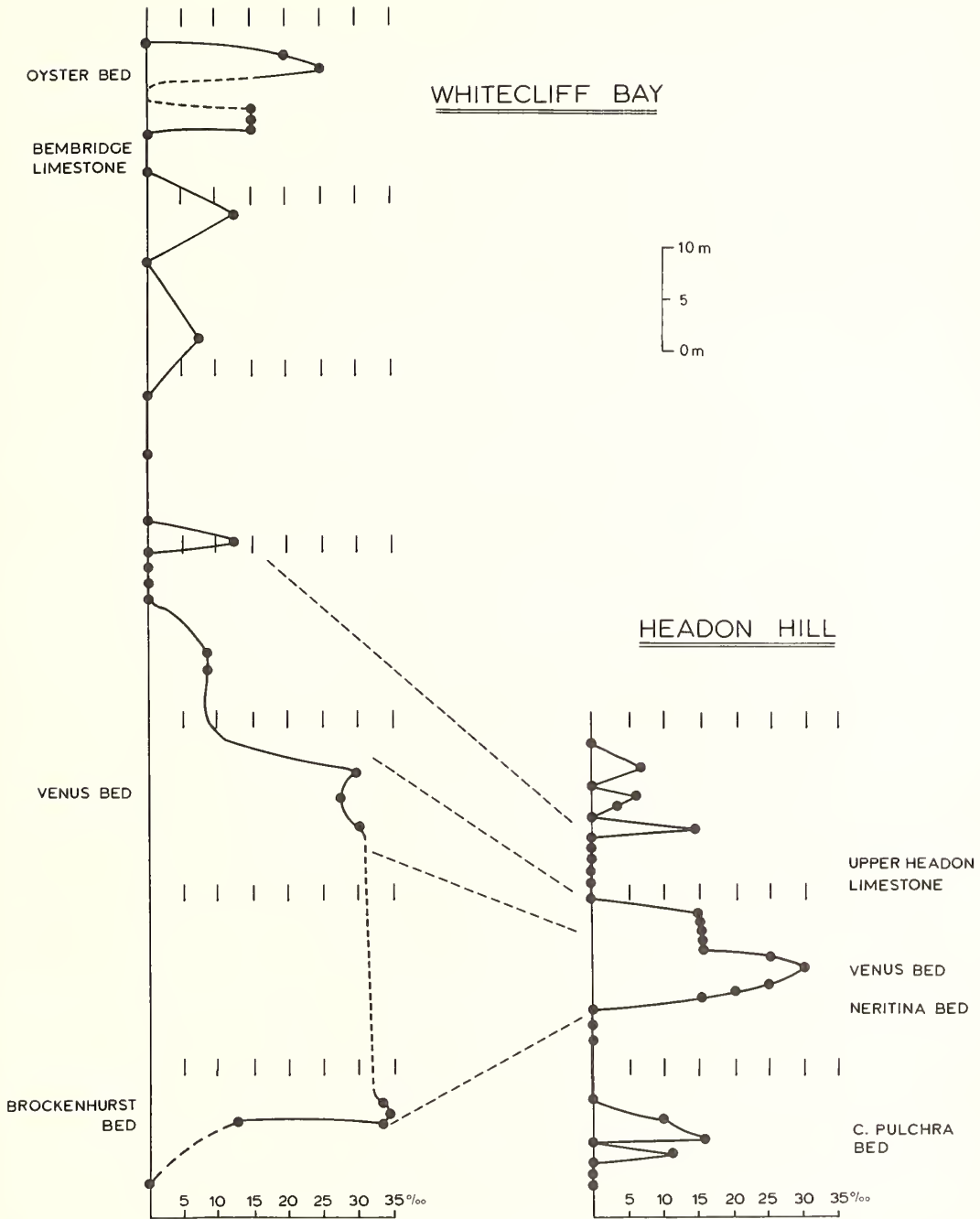
with the sea (text-fig. 8). In the polyhaline parts of the open lagoons there existed a fairly rich ostracod fauna, varying according to proximity to the sea. Oyster banks were also extensively developed. Further away from the sea connections, the water became progressively less saline, so that areas of Assemblages III and IV would be met. The fauna became poorer in number of species, but was very rich in individuals. In the mesohaline parts of the open lagoons it is probable that the 'banks' of *Batillaria ventricosa* would have been found, with the ostracod *Bradleya favosa*. Samples with worn molluscan shells and common *Haplocytheridea* and *Neocyprideis* might represent a channel connection between a closed and an open lagoon.

SALINITY PROFILES

Bearing in mind all the foregoing discussion, it is possible to allocate a salinity value to each sample. These have been plotted in text-fig. 9 to give salinity profiles for the major sections. Such profiles could be useful for correlation (see below).

DISTRIBUTION OF THE ASSEMBLAGES

The difficulty with such variable beds as these is that correlations tend to be based on facies rather than strict chronological units. For example, the Venus Beds of



TEXT-FIG. 9. Salinity profiles determined from ostracod assemblages.

Whitecliff Bay and Headon Hill are usually correlated; but in fact it is quite possible that the Venus Bed of Headon Hill is a time equivalent of the Brockenhurst Bed and Psammobia Bed. This would correlate the 'most marine' deposits of the eastern and western parts of the basin, and accepts that the marine influence becomes stronger eastwards. This is particularly apparent in the salinity profiles. At both ends of the island a fairly rapid increase in salinity is indicated, followed by a period of slightly lower salinity before returning to freshwater conditions. In the east the high salinity phase is 35‰, the lower 25‰, in the west 30‰ and 16‰. Curry (1965) has in fact suggested that the Venus Bed facies was deposited in lagoons around the Brockenhurst Sea, and Vella (1969) has correlated the Brockenhurst Bed with the Neritina Bed of Colwell Bay, and the Roydon Zone of Whitecliff Bay with the Venus Bed of Colwell Bay.

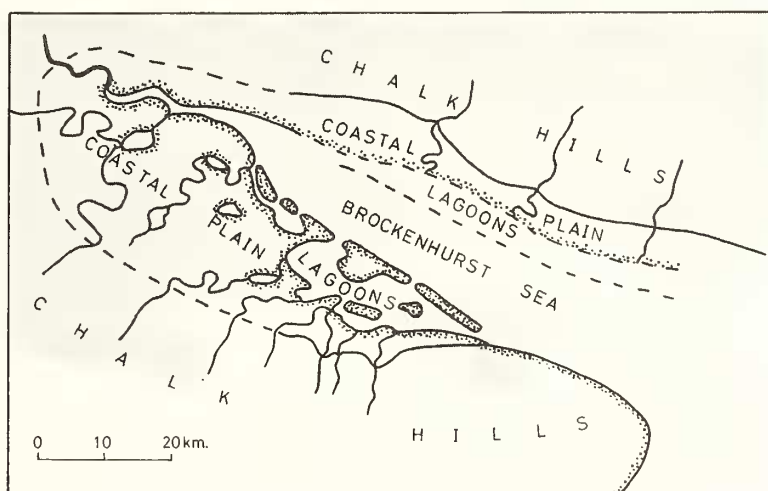
The distribution of Assemblage VI suggests that true marine conditions were only present at Whitecliff Bay and in the New Forest. Assemblage V on the other hand, is present at these localities and also at Colwell Bay, Milford, and Headon Hill. Mesohaline elements such as *Neocyprideis* are totally lacking in Assemblage V at Whitecliff Bay, while they are present at the other places, suggesting less marine influence in the west. This is also borne out by the Bembridge Oyster Bed, which contains a weakly developed Assemblage V at Whitecliff Bay, and Assemblages III and IV at Bouldnor Cliff. This bed is probably the nearest there is to a time plane throughout the whole sequence.

Assemblage IV is mainly present at the western end of the Isle of Wight. In the east it is only found in the Lower Headon Beds and the Bembridge Oyster Bed. Its principal development is in the upper part of the Middle Headon Beds and the Upper Headon Beds of Headon Hill, and it is possible that these are partly time equivalents of the development of Assemblage V in the east (i.e. the Venus Bed). Assemblage III has its main occurrence in the Upper Headon Beds and Osborne Beds of the east, but it is present in the Lower Headon Beds of the west. Once again, it is quite possible that the development of Assemblage III in the east occurred at the same time as that of Assemblages I and II in the west. Assemblage I is found in the Lower and Upper Headon Beds of the west and the Bembridge Limestone, while Assemblage II is found in the Lower Headon Beds of Paddy's Gap (Milford), and the Upper Headon Beds.

COMPARISON WITH FORAMINIFERAL STUDIES

The most detailed works published to date are those of Bhatia (1957) and Murray and Wright (1974) concerning the foraminiferal faunas. Bhatia regarded the fauna of the Brockenhurst Beds as indicating deeper-water infraneritic conditions shallowing in the Psammobia Beds. The Venus Bed was taken to indicate shallow epineritic becoming lagoonal and less saline. Murray and Wright have indicated that more modern data favours depths shallower than these. They took the foraminiferids of the Brockenhurst Beds, dominated by *Quinqueloculina*, *Triloculina*, and *Cibicides*, to indicate the seaward part of an enclosed lagoon with normal or slightly hyper-saline salinities; planktonic foraminiferids present in these beds were thought to have been transported into the lagoon from the open sea. The Venus Bed has a low

diversity of foraminiferids, and at Whitecliff Bay the succession was interpreted as showing the inner part of a hyposaline lagoon, giving way to a normal marine lagoon. At Headon Hill the foraminiferids are small, usually juveniles, so an abnormal environment was postulated, with intertidal lagoons, salinity $> 32\text{‰}$ and hyposaline subtidal lagoons or estuaries. The limestones of the Upper Headon Beds at Headon Hill yielded foraminiferids at three horizons which were taken to indicate a lagoonal environment with salinity $> 32\text{‰}$. The dominant genera are *Rosalina* and *Quinqueloculina*. The former was also found near the top of the lowermost limestone of the Bembridge Limestone at Whitecliff Bay, and interpreted as indicating very unfavourable conditions with a salinity $< 10\text{‰}$. The lowest part of the Bembridge Marls at Whitecliff Bay were interpreted as hyposaline lagoonal deposits, or an estuary, salinity 10–25‰.



TEXT-FIG. 10. The palaeogeography of the Hampshire Basin during the time of the deposition of the Brockenhurst Beds. This is intended to show the relationship between the main geographical units, and is not an exact geography. The boundaries between the coastal plain, lagoons, and sea fluctuated considerably, so that the positions of the individual lagoons and their outlets are conjectural. Evidence has been used from many sources, both consciously and subconsciously, incorporating stratigraphy, structure, sedimentation, and palaeontology. In particular, it owes much to the work of Dr. N. Edwards, although of course he may not entirely agree with the end result, and the responsibility is mine.

There seems to be close agreement between these results and those of the present study. There is a difference in interpretation of the Brockenhurst Beds, but this may be semantic because their text-fig. 28 indicates a similar interpretation to text-fig. 10 of this study. Within the hyposaline environment the ostracods offer more scope for finer detail than the Foraminifera, so that rather more environmental assemblages can be recognized. A second point of apparent disagreement is with the Upper Headon limestones of Headon Hill; Murray and Wright indicate polyhaline or

marine salinities, while this study indicates predominantly freshwater conditions. However, it has to be borne in mind that thin beds exist within the limestones that have yielded mesohaline ostracods (see text-fig. 1), while the main mass of limestone, with its abundant freshwater molluscan fauna, has not yielded any Foraminifera.

TAXONOMY

A study such as this inevitably leads to the discovery of new species. These are described in the following section. The faunal list given by Keen (1968) can now be revised as follows:

1968 name	Present name
<i>Candona</i> sp. A	<i>Candona cliffendensis</i> sp. nov.
<i>Candona</i> sp. B	<i>Candona daleyi</i> sp. nov.
<i>Cypridopsis</i> sp. A	<i>Cypridopsis hessani hantonensis</i> subsp. nov.
' <i>Eucypris</i> ' sp. A	<i>Virgatocypris edwardsi</i> sp. nov.
<i>Neocyprideis</i> cf. <i>williamsoniana</i>	<i>Neocyprideis colwellensis</i> (Jones)
<i>Brachycythere</i> sp. A	<i>Ruggieria semireticulata</i> Haskins
<i>Cushmanidea</i> sp. A	<i>Cushmanidea haskinsi</i> sp. nov.
<i>Cushmanidea</i> sp. B	<i>Cushmanidea wightensis</i> sp. nov.
<i>Haplocytheridea</i> sp. A	<i>Haplocytheridea mantelli</i> Keen
<i>Limmocythere</i> sp. A	<i>Cladarocythere hantonensis</i> Keen
<i>Paracytheridea</i> sp. A	<i>Paracytheridea gradata</i> (Bosquet)
<i>Schuleridea</i> sp. A	<i>Schuleridea perforata headonensis</i> subsp. nov.

SYSTEMATIC DESCRIPTIONS

The classification is that of the *Treatise* (Moore 1961). In the descriptions, the heading 'Material' refers to the total sample examined; the numbers refer to individual specimens deposited at the British Museum (Natural History), prefixed Io.

Abbreviations. L = length, H = height, W = width; measurements are in millimetres.

Order PODOCOPIIDA Muller, 1894
 Suborder PODOCOPINA Sars, 1866
 Superfamily CYPRIDACEA Baird, 1845
 Family CYPRIDIDAE Baird, 1845
 Genus CYPRIDOPSIS Brady, 1868
Cypridopsis hessani Carbonnel and Ritzkowski, 1969
Cypridopsis hessani hantonensis subsp. nov.

Plate 46, figs. 9-11

1975 *Cypridopsis* sp. A, Keen, p. 275.

Derivation of name. After Hampshire.

Type locality. Upper Headon Beds, Headon Hill (HH53).

Distribution. Sample HH53 only.

Holotype. Io 6736, female left valve.

Material. Over 100 valves. Registered specimens Io 6736-6739.

Dimensions. Holotype, female left valve, Io 6736: L, 0.44; H, 0.25; L/H, 1.76; W/2, 0.11. Female right valve, Io 6737: L, 0.43; H, 0.24. Male left valve, Io 6738: L, 0.44; H, 0.23; L/H, 1.91; W/2, 0.10. Male right valve, Io 6739: L, 0.44; H, 0.23.

Diagnosis. Small, elongate, small denticles along anterior margin of right valve.

Description and discussion. The nominate subspecies was described from the Melanenton (Rupelian) of Hesse, Germany; it differs from the present subspecies by its large size (0.53 cf. 0.44) and in details of lateral outline. Carbonnel and Ritzkowski were unable to recognize sexual dimorphism; the L/H ratio given by them, 1.88, is closer to that of the male in the Headon samples, but as there are differences in lateral outline, and because it is virtually unknown to have a sample consisting of males only, it is advisable to compare the nominate subspecies with both sexes. The female left valve of *C. hessani hantonensis* differs in having a well-defined highest point with an evenly curved antero-dorsal margin; the male left valve has a more evenly curved dorsal margin, lacking the cardinal angles of *C. hessani hessani*. Sexual dimorphism is not as prominent in the right valve; the ventral margin is more concave than in *C. h. hessani*.

Internal details as for the genus; the central muscle scars cannot be clearly seen, but appear to be typical of *Cypridopsis*; large anterior vestibule present, with numerous short radial pore canals.

GENUS VIRGATOCYPRIS Malz and Moayedpour, 1973

Virgatocypris edwardsi sp. nov.

Plate 47, figs. 3, 6, 9, 12

1968b ?*Scottia* sp. Haskins, p. 5, pl. 1, figs. 7-9.

1975 *Eucypris* cf. *temuistriata* (Dollfus); Keen, p. 272.

Derivation of name. In honour of Dr. N. Edwards.

Type locality. Lower Headon Beds, Headon Hill (HH23).

Distribution. Lower and Upper Headon Beds of Headon Hill and Colwell Bay.

Holotype. Io 6740, a left valve.

Material. Eight complete adult valves, several fragments, forty-five larval stages. Registered specimens Io 6740-6743.

Dimensions. Holotype, left valve, Io 6740: L, 1.13; H, 0.65; L/H, 1.72. Right valve, Io 6741: L, 1.16; H, 0.66; L/H, 1.76.

Diagnosis. Dorsal margin with prominent, pointed, highest point; ventral margin convex.

Description. See Plate 47, figs. 3, 9 for lateral outline. The valves are swollen ventrally. The surface of the valve has fine longitudinal striations; no unornamented specimens have been observed. Internally features are as for the genus: a conspicuous selvage, large anterior vestibule, numerous straight radial pore canals; the central muscle scars have not been clearly observed.

Discussion. This differs from other species principally in lateral outline. *V. tenuistriata* (Dollfus) (Oligocene, Paris Basin) is more elongate and ovoid; *V. straubi* (Carbannel and Ritzkowski) (Oligocene, Hesse) has its highest point nearer anterior and has a pronounced concave ventral margin in the right valve; *V. virgata* Malz and Moayedpour (Miocene, Germany) is more elongate, has a straighter dorsal margin, and a straight ventral margin; *V. grisyensis* (Margerie) (Upper Eocene, Paris Basin) is smaller, has a weakly developed selvage, and has its highest point placed medianly giving a symmetrically curved dorsal margin. The exact pattern of striations also appears to differ amongst these species.

The specimens of *Virgatocypris* from the Bembridge Limestone have been left in open nomenclature. They differ from the Headon forms in being slightly more elongate, having a less-pointed dorsal margin, and a slightly more tapered posterior. Jones and Sherborn (1889, p. 43) described a new species from the Bembridge Limestone of West Cowes, *Pseudocythere bristovi*, which might be a species of *Virgatocypris*. Two specimens of this species are preserved in the collections of the Institute of Geological Sciences, Mik (T) 712 001 and 712 002, neither being type material. The specimens are incomplete, in limestone, and their identity difficult to determine; they are not the same as the Headon species, however.

Family CANDONIDAE Kaufmann, 1900

Genus CANDONA Baird, 1845

Candona cliffendensis sp. nov.

Plate 46, figs. 6-8

- ‡1889 *Pontocypris* (?) sp. Jones and Sherborn, p. 16, pl. 1, fig. 13a.
 1968b ?*Candonopsis* sp. Haskins, p. 7, pl. 2, figs. 23-27.
 1975 *Candona* (*Pseudocandona*) sp. B. Keen, p. 272.

Derivation of name. After the type locality.

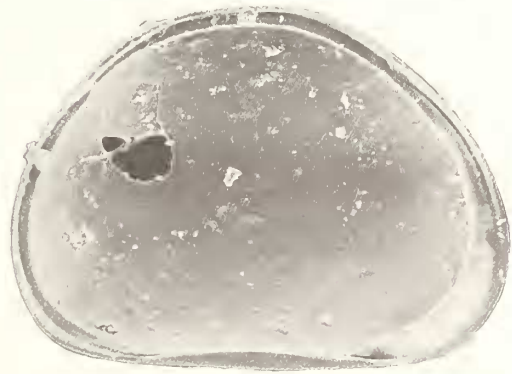
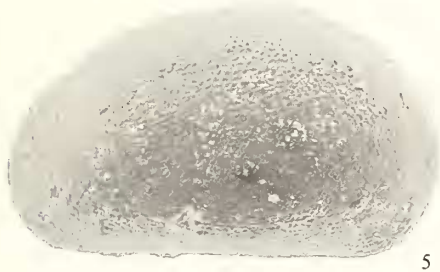
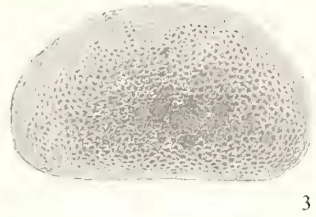
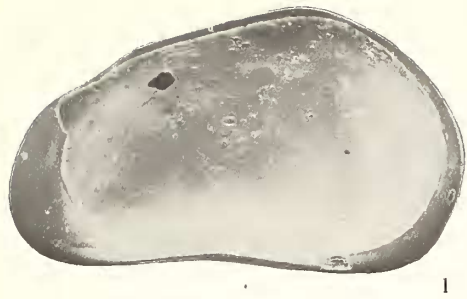
Type locality. Upper Headon Beds, Cliff End (Colwell Bay, CB12).

Distribution. Lower and Upper Headon Beds of Headon Hill and Colwell Bay; Osborne and Bembridge Beds of Whitecliff Bay.

Holotype. Io 6744, a left valve.

EXPLANATION OF PLATE 46

- Figs. 1-5. *Candona daleyi* sp. nov. 1, 2, holotype, Io 6747, Lower Headon Beds of Headon Hill. 1, right valve internal view, $\times 70$. 2, central muscle scars, $\times 450$. 3-5, Upper Headon Beds of Colwell Bay (CB12), $\times 70$. 3, left valve of moult no. 7, Io 6749. 4, right valve of moult no. 7, Io 6750. 5, left valve of moult no. 8, Io 6748.
- Figs. 6-8. *Candona cliffendensis* sp. nov. 6, Upper Headon Beds of Headon Hill (HH53), left valve of moult no. 7, Io 6746, $\times 70$. 7, 8, Upper Headon Beds of Colwell Bay (CB12). 7, right valve internal view, specimen destroyed, $\times 70$. 8, stereo-pair, right valve of holotype, $\times 50$.
- Figs. 9-11. *Cypridopsis hessani hantonensis* subsp. nov., Upper Headon Beds of Headon Hill (HH53), $\times 140$. 9, holotype, female left valve, Io 6736. 10, male left valve, internal view, Io 6738. 11, female right valve, Io 6737.
- Fig. 12. *Cypria dorsalta* Malz and Moayedpour, left valve, internal view, Io 6734, Lower Headon Beds of Headon Hill (HH30), $\times 125$ (L = 0.54 mm).



KEEN, Upper Eocene ostracods

Material. Six adult valves, forty larval stages. Registered specimens Io 6744–6746.

Dimensions. Holotype, right valve, Io 6744: L, 0.84; H, 0.41; L/H, 2.05; left valve, Io 6745: L, 0.85; H, 0.42; L/H, 2.02. Larval 8, right valve, Io 6746: L, 0.68; H, 0.34; L/H, 2.00. Larval 7, right valve, Io 6746: L, 0.50; H, 0.24; L/H, 2.05.

Diagnosis and description. For lateral outline see Plate 46, figs. 7–9. L/H 2.00; larval stages smooth. Internal details as for the genus.

Discussion. This is distinguished from other Tertiary species by its elongate shape and smooth larval stages (see *C. daleyi* below for discussion). The anterior and posterior cardinal angles suggest it belongs to *Candona* rather than *Candonopsis* Vavra, although the elongate shape is more characteristic of the latter.

Candona daleyi sp. nov.

Plate 46, figs. 1–5

1968b *Potamocypris* sp. Haskins, p. 6, pl. 1, figs. 17–22.

1975 *Candona* (*Pseudocandona*) sp. A, Keen, p. 272.

Derivation of name. In honour of Dr. B. F. Daley.

Type locality. Lower Headon Beds, Headon Hill (HH23).

Distribution. Lower and Upper Headon Beds and Osborne Beds of Headon Hill, Colwell Bay, Whitecliff Bay; Middle Headon Beds of Headon Hill; Bembridge Limestone of Whitecliff Bay and Bouldnor Cliff.

Holotype. Io 6747, a right valve.

Material. Two adult right valves, numerous larval stages. Registered specimens Io 6747–6750.

Dimensions. Holotype, right valve, Io 6747: L, 0.87; H, 0.55; L/H, 1.58. Larval 8, left valve, Io 6748: L, 0.81; H, 0.52. Larval 8, right valve: L, 0.75; H, 0.46. Larval 7, left valve: Io 4749: L, 0.58; H, 0.36. Larval 7, right valve: Io 4750: L, 0.53; H, 0.33.

Diagnosis. Highest point near posterior; distinct antero-dorsal notch seen in lateral view; L/H 1.58; larval stages punctate.

EXPLANATION OF PLATE 47

Figs. 1, 2. *Cushmanidea stintoni* sp. nov., $\times 120$, Middle Headon Beds of Headon Hill. 1, left valve of female, holotype, Io 6766. 2, right valve of female, Io 6767.

Figs. 3, 6, 9, 12. *Virgatocypris edwardsi* sp. nov. 3, 6, holotype, Io 6740, Lower Headon Beds of Headon Hill. 3, stereo-pair, left valve, $\times 48$. 6, stereo-pair, enlargement showing simple normal pore canals with rims, $\times 300$. 9, 12, Upper Headon Beds of Colwell Bay (CB12). 9, right valve, Io 6741, $\times 48$. 12, internal view of right valve, Io 6742, $\times 55$.

Fig. 4. *Cushmanidea haskinsi* sp. nov., $\times 84$, left valve of female, holotype, Io 6761, Middle Headon Beds of Headon Hill.

Figs. 5, 7, 10, 13. *Cushmanidea wightensis* sp. nov., $\times 70$, Middle Headon Beds of Headon Hill. 5, left valve of male, Io 6773. 7, left valve of female, holotype, Io 6771. 10, right valve of female, Io 6772. 13, internal view of male left valve, Io 6774.

Fig. 8. *Loxoconcha* sp., L = 0.48, left valve, Io 6783, Middle Headon Beds of Headon Hill.

Figs. 11, 14. *Cytherura pulchra* sp. nov., $\times 100$, Lower Headon Beds of Headon Hill. 11, right valve, Io 6777. 14, left valve, holotype, Io 6776.

Fig. 15. *Idiocythere bartoniana* Haskins, L = 0.47, right valve, Io 6781, Brockenhurst Beds of Whitecliff Bay.



KEEN, Upper Eocene ostracods

Description. For lateral outline see Plate 46, fig. 1. Adult right valve has a prominent rim around the anterior, ventral, and posterior margins. Surface is smooth in adult, punctate in larval stages. Internal details as for the genus. The right valve of the penultimate larval stage has a similar outline to the adult, including the antero-dorsal notch; the left valve of the penultimate larval stage may therefore indicate the outline of the left valve of the adult.

Discussion. According to Triebel (1963) this species should be placed in the subgenus *Candona* (*Pseudocandona*) Kaufmann, 1900, on account of the punctate larval stages. However, recent opinion (especially Dr. R. Meyrick, pers. comm. 1974) would only separate these on soft-part morphology. Thus, no subgeneric status is designated. *C. daleyi* differs from *C. fertilis* Triebel in lateral outline, especially the presence of the antero-dorsal notch, and in the presence of a marginal rim.

The larval stages of this species are very common in freshwater sediments of the Headon-Bembridge series; they are distinguished from larval *C. cliffendensis* by being shorter and punctate, and from the undescribed species from the Hamstead Beds (Keen 1972a, p. 283, pl. 47, fig. 8) by being shorter.

Superfamily CYTHERACEA Baird, 1850
Family CYTHERIDEIDAE Sars, 1925
Subfamily CYTHERIDEINAE Sars, 1925
Genus NEOCYPRIDEIS Apostolescu, 1956
Neocyprideis colwellensis (Jones)

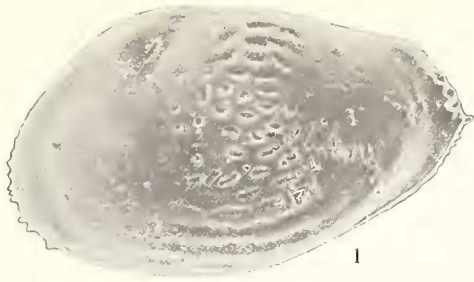
Plate 48, figs. 5-12

- 1857 *Cytherideis colwellensis* Jones (pars), p. 49, pl. 14, fig. 13.
1889 *Cytherideis colwellensis* Jones; Jones and Sherborn (pars), p. 45.
1960 *Neocyprideis* aff. *williamsoniana* (Bosquet); Kollmann, p. 177, pl. 3, fig. 2a-b; pl. 12, fig. 8; pl. 20, figs. 8-10.
1969 *Cyprideis* (*Neocyprideis*) *williamsoniana* (Bosquet); Haskins, p. 155, pl. 4, figs. 10-20.

Type locality and distribution. Colwell Bay; Headon-Osborne Beds.

EXPLANATION OF PLATE 48

- Fig. 1. *Ruggieria semireticulata* Haskins, L = 0.88, left valve, Io 6780, Middle Headon Beds of Whitecliff Bay (WB22).
Fig. 2. *Pokornyella osnabrugensis* (Lienenklaus), L = 0.59, right valve, Io 6782, Middle Headon Beds of Headon Hill (HH43).
Figs. 3, 4. *Hazelina indigena* Moos, Brockenhurst Beds of Whitecliff Bay. 3, right valve of female, Io 6778, L = 0.54. 4, right valve of male, Io 6779, L = 0.57.
Figs. 5-12. *Neocyprideis colwellensis* (Jones), all specimens from Headon Hill, figs. 5, 11 from Upper Headon Beds (HH58), remainder from Middle Headon Beds (HH48). 5, left valve of male of a smooth form, Io 6753, $\times 55$. 6, stereo-pair, right valve of female punctate form, Io 6751, $\times 55$. 7, stereo-pair, right valve of male punctate form, Io 6752, $\times 55$. 8, stereo-pair, left valve of moult no. 8 showing development of nodes, note that each 'node' is in fact a cluster of small nodes, Io 6755, $\times 75$. 9, detail of anterior part of hinge of Io 6754 (see also fig. 10), $\times 350$. 10, internal view of female right valve, Io 6754, $\times 55$. 11, sieve type normal pore canal of Io 6753 (see also fig. 5), $\times 1300$. 12, central muscle scars of Io 6754 (see also fig. 10), $\times 300$.



KEEN, Upper Eocene ostracods

Lectotype. BM(NH), I 6431 (13). Jones figured two species under the name *Cytherideis colwellensis*; one has subsequently been described as *Cytheretta rhenana headonensis* Haskins, 1968. Keen (1972a) and Malz (1973) independently chose the remaining specimen as the lectotype of *Neocyprideis colwellensis*. The specimen is a larval stage, but adult topotype material is abundant.

Material. Registered specimens Io 6751–6755.

Diagnosis. Has similar-sized valves, males and females have similar L/H ratios, female carapace inflated at posterior end; anterior and median hinge elements of equal length; twenty anterior radial pore canals; surface with dorsal sulcus.

Discussion. There are nine described species of *Neocyprideis* ranging from the upper Cretaceous to the Miocene. Many of these form part of a continuous phyletic lineage, which makes specific determination difficult unless there is sufficient material for population studies. The two species most closely resembling *N. colwellensis* are *N. apostolescui* (Keij), thought to be its ancestor, and *N. williamsoniana* (Bosquet), which is probably its descendant. Specimens from the Bembridge Beds have been placed in the latter. *N. apostolescui* differs in having a more evenly rounded anterior end when seen in lateral view, has a more curved anterior hinge element which is shorter than the median element, and has fewer anterior radial pore canals (16–19 cf. 17–24). Keij (1957) used the absence of a punctate surface to differentiate *N. apostolescui* from *N. williamsoniana*; as indicated earlier, this character is probably phenotypic, and all species of *Neocyprideis* may be smooth or punctate. *N. williamsoniana* differs from *N. colwellensis* in having more clearly differentiated sexes using L/H measurements, a more angular postero-dorsal angle, especially when viewed from the inside of the valve, a weaker dorsal sulcus, and the posterior inflation of the female carapace is situated in a more dorsal position.

Noding. *N. colwellensis* has ten node positions (text-fig. 11), although several of these are frequently joined by the development of smaller nodes between them. A node may be a single tubercle, or a cluster of small tubercles (Pl. 48, fig. 8). All nodes are present in the adult and instars 7 and 8, but earlier instars have fewer nodes, although there does not seem to be any orderly appearance of nodes during ontogeny. Nodes are present on both valves and both sexes with equal frequency.

EXPLANATION OF PLATE 49

Figs. 1–4. *Schuleridea (Aequacytheridea) perforata headonensis* subsp. nov., $\times 70$, Middle Headon Oyster Bed of Colwell Bay. 1, left valve of female, holotype, Io 6756. 2, right valve of female, Io 6757. 3, left valve of male, Io 6759. 4, internal view of left valve of female, Io 6758.

Figs. 5, 6. *Eocytheropteron wetherelli* (Jones), L = 0.70, Middle Headon Beds of Headon Hill (HH43), stereo-pairs. 5, female right valve. 6, normal pore canal showing a larger central pore within the sieve-type pore canal, $\times 1500$.

Figs. 7, 8. *Leguminocythereis delirata* (Jones and Sherborn), L = 0.82, Middle Headon Beds of Headon Hill (HH43). 7, normal pore canals showing a larger central pore within the sieve-type pore canal, $\times 400$. 8, female left valve.

Figs. 9, 10. *Cytheromorpha bulla* Haskins, L = 0.64, Lower Headon Beds of Headon Hill (HH26). 9, female left valve. 10, stereo-pair showing sieve-type normal pore canals, $\times 170$.



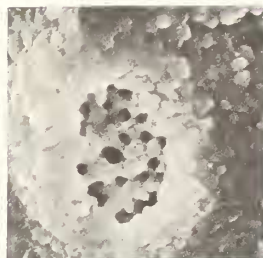
1



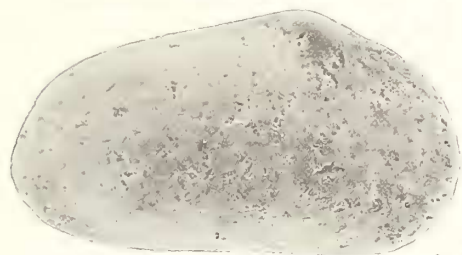
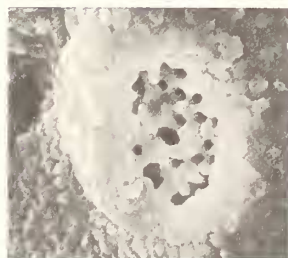
5



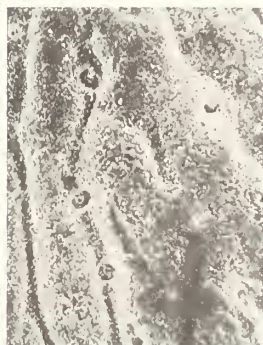
2



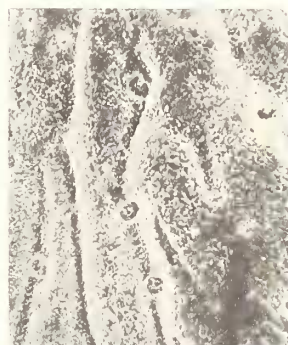
3



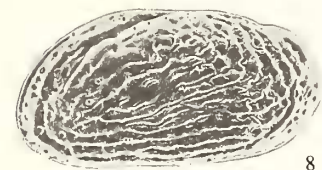
3



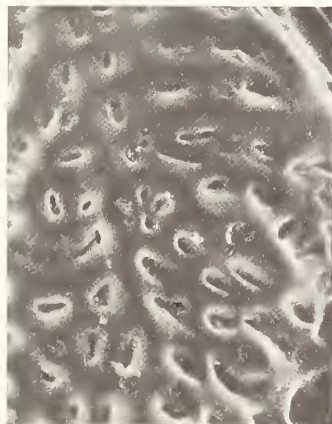
7



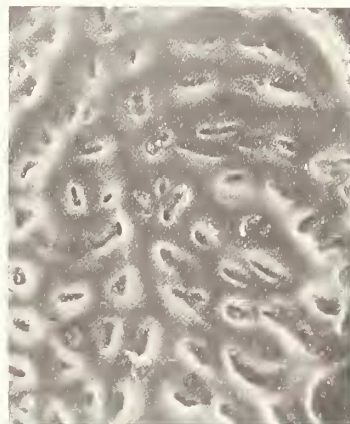
4



8

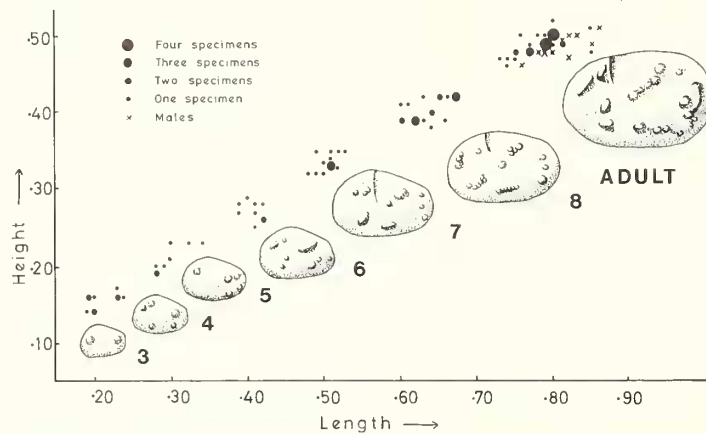


9



9

Larval stages. Six juvenile stages have been recognized; text-fig. 11 shows the changes in lateral outline during ontogeny; note the triangular outline with highest point at anterior in the early stages. A punctate surface has been observed in instars 7 and 8, but earlier instars are smooth. The hinge elements are crenulate for instars 6, 7, and 8 and appear to be so for earlier instars. The median element occupies more than 50% of the hinge length in instars 3–7, with a reduced anterior element; the latter increases for instar 8 and is equal to the median element in the adult. The posterior hinge element retains a similar proportion throughout ontogeny. The number of radial pore canals increases during ontogeny from an average of six in instar 4 to twenty in the adult. These changes during ontogeny parallel the changes seen in phylogeny.



TEXT-FIG. 11. Size distribution of *Neocyprideis colwellensis* (Jones) from the Cyrena pulchra Bed (Lower Headon Beds) of Headon Hill (HHCP2).

Genus SCHULERIDEA Swartz and Swain, 1946

Subgenus SCHULERIDEA (AEQUACYTHERIDEA) Mandlestam, 1947

Schuleridea (Aequacytheridea) perforata (Roemer)

Schuleridea (Aequacytheridea) perforata headonensis subsp. nov.

Plate 49, figs. 1–4

1857 *Cytheridea perforata* Roemer; Jones, p. 44 (pars), pl. IV, fig. 14a–e.

1889 *Cytheridea perforata* Roemer; Jones and Sherborn, p. 39 (pars).

1969 *Schuleridea perforata* (Roemer); Haskins, p. 161 (pars).

Derivation of name. After the Headon Beds.

Type locality. Colwell Bay (Oyster Bed).

Distribution. Venus Bed of Headon Hill, Colwell Bay, and Whitecliff Bay.

Holotype. Io 6756, a female left valve.

Material. Forty-seven valves. Registered specimens Io 6756–6760.

Dimensions. Mean of eleven female left valves: L, 0.82; H, 0.53; L/H, 1.56. Mean of three male left valves: L, 0.89; H, 0.52; L/H, 1.70.

Diagnosis. Pronounced sexual dimorphism, elongate carapace, prominent posterior cardinal angle, no marginal spines or denticles, surface finely punctate.

Discussion. According to the literature *S. (A.) perforata* is one of the most widely ranging species of ostracods in a stratigraphical sense; it is found from the Palaeocene to Miocene. Moos (1970) and Malz (1973) have shown how it is possible to recognize distinct species and subspecies by careful study of the lateral outline and ornamentation. Internal features do not vary greatly, and the new subspecies is very similar to the nominate subspecies in this respect. *S. (A.) perforata headonensis* differs in being more elongate and showing more distinct sexual dimorphism: L/H female 1.56 cf. 1.47 (*S. (A.) perforata perforata* from Damery), male 1.70 cf. 1.57. The dorsal margin has a more pronounced posterior cardinal angle; the nominate subspecies almost lacks this, and so has a more tapered and triangular appearance. The posterior margin of the nominate subspecies is pointed, which in *S. (A.) perforata headonensis* it is not. The ventral margin is straight to convex, while the nominate subspecies is straight to concave. The surface is punctate, but this ornamentation does not often show very clearly because of the mode of preservation.

Subfamily NEOCYTHERIDEIDINAE Puri, 1957

Genus CUSHMANIDEA Blake, 1933

Cushmanidea haskinsi sp. nov.

Plate 47, fig. 4

- 1857 *Cytherideis flavida* Jones (non Muller), p. 50 (pars).
 1889 *Cytherideis* sp. Jones and Sherborn, p. 45.
 ?1970 *Cushmanidea grosjeani* Haskins (non Keij), p. 16 (pars), pl. 1, figs. 16, 18, 19, 21.
 ?1970 *Cushmanidea* sp. Haskins, p. 16, pl. 1, figs. 22-23.

Derivation of name. In honour of Dr. C. W. Haskins.

Type locality. Middle Headon Beds (Venus Bed), Headon Hill.

Distribution. Venus Bed of Headon Hill, Oyster Bed of Colwell Bay, and ?Middle Headon Beds of Whitecliff Bay.

Holotype. Io 6761, a female left valve.

Material. Seventeen valves and carapaces. Registered specimens Io 6761-6765.

Dimensions. Female carapace, Io 6764: L, 0.62; H, 0.27; W, 0.25; L/H, 2.30. Male carapace, Io 6765: L, 0.72; H, 0.28; W, 0.26; L/H, 2.57.

Diagnosis. Elongate, eight to nine faint ridges parallel to anterior margin, large anterior and narrow posterior vestibules, radial pore canals simple.

Description. For outline and ornamentation see figured specimen. Note the eight to nine weak ridges developed in the anterior and antero-ventral areas, and running parallel to the anterior margin. There are some sixty normal pore canals which widen near the outer surface and appear to be of the sieve-type.

Internally, all the hinge elements are smooth; the duplicature has large anterior and narrow posterior vestibules, with 26 anterior, 16 ventral, and 7 posterior radial pore canals; the selvage is parallel to the outer margin. The central muscle scars consist of a row of 4 scars, the dorsal-most of which is usually indistinct; the frontal scar is irregular, but tendency towards a V shape; there are 2 small mandibular scars, and some 7 dorsal muscle scars.

Discussion. *C. lithodomoides* (Bosquet) has a similar ornamentation, differing by its stronger development and the ridges running parallel to the outer margin so that they are parallel to the ventral margin in their ventral portion. The closest species is *C. therwilensis* (Oertli) from the upper Oligocene of Switzerland; the ornamentation and internal features are very similar. The main difference is in lateral outline; the highest point is much nearer the posterior in *C. therwilensis*, and the posterior margin is more pointed. The material described by Haskins probably belongs here although his specimens are larger. The forms referred to as *C. grosjeani* are probably females, and *Cushmanidea* sp. the males.

Cushmanidea stintoni sp. nov.

Plate 47, figs. 1, 2

1970 *Cushmanidea grosjeani* Haskins (non Keij), (pars), p. 16, pl. 1, figs. 17, 20.

Derivation of name. In honour of Mr. F. C. Stinton, a worker on Tertiary otoliths and guide to the Tertiary of Hampshire.

Type locality. Middle Headon Beds (Venus Bed), Headon Hill.

Distribution. Venus Bed of Headon Hill, Middle Headon Beds and Bembridge Marls Oyster Bed of Whitecliff Bay.

Holotype. Io 6766, a female left valve.

Material. Twenty-four valves and carapaces. Registered specimens Io 6766-6770.

Dimensions. Female carapace, Headon Hill, Io 6768: L, 0.53; H, 0.23; W, 0.21; L/H, 2.30. Female carapace, Whitecliff Bay, Io 6769: L, 0.65; H, 0.27; W, 0.23; L/H, 2.33. Male carapace, Whitecliff Bay, Io 6770: L, 0.69; H, 0.26; W, 0.26; L/H, 2.62.

Diagnosis. Small, prominent pits at posterior, medium-sized anterior vestibule, simple radial pore canals.

Description. For lateral outline and ornamentation see figured specimens. Each of the pits seen on the surface of the carapace has a sieve-type normal pore canal opening into it. Viewed with an optical microscope, the pits are seen as being predominantly at the posterior, with a lesser development along the venter and anterior.

Internally, all hinge elements are smooth, the anterior and median elements of about equal length. The anterior vestibule is of medium size, ventral and posterior vestibules small. There are 35 anterior, 16 ventral, and 10 posterior simple radial pore canals; the selvage is parallel to outer margin. Central muscle scars a row of 4, dorsal-most is large; a single V-shaped frontal scar; 2 small mandibular scars.

Sexual dimorphism is apparent in the specimens from Whitecliff Bay, but not in those from Headon Hill; all the latter are presumed to be females. The Whitecliff Bay specimens are also larger, but otherwise identical.

Discussion. The most similar species is *C. neauphlensis* (Apostolescu) from the Lutetian of the Paris Basin. This differs in lateral outline, with its highest point slightly to the anterior of the mid-point, has strong pitting over the entire surface, and a median dorsal sulcus. Keij (1957) placed *C. neauphlensis* in the synonymy of *C. mayeri* (Howe and Garrett) from the Eocene of the U.S.A.; certainly the two species are very similar.

Cushmanidea wightensis sp. nov.

Plate 47, figs. 5, 7, 10, 13

Derivation of name. From the Isle of Wight.

Type locality. Middle Headon Beds (Venus Bed), Headon Hill.

Distribution. Venus Bed of Headon Hill, Oyster Bed of Colwell Bay.

Holotype. Io 6771, a female left valve.

Material. Twenty-two valves. Registered specimens Io 6771–6775.

Dimensions. Female carapace, Io 6775: L, 0.64; H, 0.33; W, 0.29; L/H, 1.94. Male left valve, Io 6773: L, 0.77; H, 0.34; L/H, 2.26.

Diagnosis. Not particularly elongate, unornamented, hinge elements crenulate, no vestibules, simple radial pore canals.

Description. For lateral outline seen figured specimens. Sexual dimorphism is very pronounced, although males are rare (3 out of 22 specimens). Right valve more pointed dorsally. There are 55–60 normal pore canals.

Internally, the hinge is crenulate; the anterior element has some 5 coarse denticles, median element very finely crenulate, posterior element coarse, with 6–7 denticles. Ratio of hinge-element lengths, anterior:median:posterior, 3:3:2. There are no vestibules; 16 anterior, 6 ventral, and 4 posterior simple radial pore canals; there is a suggestion in one specimen of a series of blind ventral radial pore canals. Central muscle scars consist of a vertical row of 4, all in contact, with 2 frontal scars very close together and often appearing as a single V-shaped scar. There is a prominent fulcral point, and 2 large mandibular scars.

Discussion. There are no other species with which to compare, and it is doubtful whether this is a true *Cushmanidea* species, because of the lack of vestibules and crenulate hinge.

Family CYTHERURIDAE G. W. Muller, 1894

Genus CYTHERURA Sars, 1866

Cytherura pulchra sp. nov.

Plate 47, figs. 11, 14

Derivation of name. After the *Cyrena pulchra* Bed.

Type locality. The *Cyrena pulchra* Bed, Headon Hill.

Distribution. Only recorded in the type deposit of Headon Hill.

Holotype. Io 6776, a left valve.

Material. Twenty-four valves and several fragments.

Dimensions. Holotype, left valve, Io 6776: L, 0.38; H, 0.18; right valve, Io 6777: L, 0.39; H, 0.19.

Diagnosis. Small, elongate, strong caudal process, surface reticulate, weak longitudinal ridges developed, right valve larger.

Description. Sexual dimorphism cannot be clearly recognized; occasional shorter specimens (0.35 mm) may be females, in which case most of the material consists of males. Although there are not enough specimens to be sure, the right valve appears to be the larger. The surface ornamentation varies in strength between specimens, and is reticulate; there is a tendency for a weak median and ventral ridge to develop. In juveniles the reticulation is more regular, though much weaker, and the surface appears to be punctate. Internally the hinge is as for the genus, the duplicature has a few wavy radial pore canals; the central muscle scars cannot be seen.

Discussion. Externally this is similar to several species now placed in *Semicytherura*: *S. dunkeri* Moos (Melanienton, North Germany), *S. gracilis* (Lienenklaus) (Rupelian, Paris Basin), and *S. oedelemensis* (Keij) (Eocene–Oligocene). It differs in details of ornamentation and shape, as well as in internal details.

Acknowledgements. I thank Drs. B. Daley and N. Edwards for reading a draft of the manuscript and for valuable discussions. I am indebted to Mr. R. Cumberland (Geology Department, Glasgow University) for running the computer program and to Mr. G. McTurk (Geology Department, Leicester University) for the stereoscan photographs.

REFERENCES

- APOSTOLESKU, V. 1956. Contribution à l'étude des Ostracodes de l'Eocene inférieur (s.l.) du Bassin de Paris. *Revue Inst. fr. Petrole.* **11**, 1327–1352, pls. 1–4.
- BAIRD, W. 1845. Arrangement of the British Entomostraca. *Hist. Berwicksh. Nat. Club.* 145–148.
- BARKER, D. 1963. Size in relation to salinity in fossil and recent euryhaline ostracods. *J. mar. biol. Ass. U.K.* **43**, 785–795.
- BENDA, W. K. and PURI, H. S. 1962. The distribution of Foraminifera and Ostracoda off the Gulf of the Cape Romano area, Florida. *Trans. Gulf-Cst Ass. geol. Soc.* **12**, 303–341.
- BHATIA, S. B. 1957. The Paleocology of the Late Paleogene sediments of the Isle of Wight, England. *Contr. Cushman Fdn. foramin. Res.* **8**, 11–28.
- BLAKE, C. 1933. Order Ostracoda in Biol. Surv. Mount Desert Region, dir. W. Proctor. *West. Inst. Anat. Biol.*, pt. V, 229–241, figs. 39–40.
- BONHAM-CARTER, G. F. 1967. Fortram IV program for Q mode cluster analysis of non-quantitative data using IBM 7090/7094 computers. *Kansas Geol. Survey Computer Contr.* No. 17, 1–28.
- BRADY, G. S. 1868. A monograph of the Recent British Ostracoda. *Trans. Linn. Soc. Lond.* **26**, 353–495, pls. 23–41.
- CARBONNEL, G. 1969. Les ostracodes du Miocene Rhodanien. *Docum. Lab. geol. Fac. Sci. Lyon*, No. 32, 1, 228 pp., 16 pls.
- and RITZKOWSKI, S. 1969. Ostracodes lacustres de l'Oligocène. *Arch. Sci. Genève*, **22**, 55–82, pls. 1–5.
- CHEETHAM, A. H. and HAZEL, J. 1969. Binary (presence-absence) similarity coefficients. *J. Paleont.* **43**, 1130–1136.
- CURRY, D. 1965. The Palaeogene Beds of South-east England. *Proc. Geol. Ass.* **76**, 151–174.
- CURTIS, D. M. 1960. Relation of environmental energy levels and ostracod biofacies in east Mississippi Delta area. *Bull. Am. Ass. Petrol. Geol.* **44**, 471–494.
- DALEY, B. 1972. Macroinvertebrate assemblages from the Bembridge Marls (Oligocene) of the Isle of Wight, England, and their environmental significance. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **11**, 11–32.
- 1973. The palaeoenvironment of the Bembridge Marl (Oligocene) of the Isle of Wight, Hampshire. *Proc. Geol. Ass.* **84**, 83–93.
- and EDWARDS, N. 1971. Palaeogene warping in the Isle of Wight. *Geol. Mag.* **108**, 399–405.
- EDWARDS, N. 1967. Oligocene studies in the Hampshire Basin. *Thesis*, Univ. of Reading, 170 pp., unpublished.
- 1971. Stratigraphy and correlation of the Headon, Osborne, Bembridge, and Hamstead Beds (Palaeogene), Hampshire Basin—a bibliography (1914–1970). *J. Soc. Bibliophy nat. Hist.* **6**, 50–60.

- ENGEL, P. L. and SWAIN, F. M. 1967. Environmental Relationships of Recent Ostracoda in Mesquite, Aransas and Copano Bays, Texas Gulf Coast. *Trans. Gulf-Cst Ass. geol. Soc.* **17**, 408-427.
- FORBES, E. 1853. On the fluviomarine Tertiaries of the Isle of Wight. *Jl geol. Soc. Lond.* **9**, 259-270.
- 1856. On the Tertiary Fluvio-marine Formation of the Isle of Wight. *Mem. geol. Surv. U.K.* 162 pp.
- HASKINS, C. W. 1968a. Tertiary ostracoda from the Isle of Wight and Barton, Hampshire, England. Part I. *Revue Micropaleont.* **10**, 250-260, 2 pls.
- 1968b. Tertiary ostracoda from the Isle of Wight and Barton, Hampshire, England. Part II. *Ibid.* **11**, 3-12, 2 pls.
- 1968c. Tertiary ostracoda from the Isle of Wight and Barton, Hampshire, England. Part III. *Ibid.* 161-175, 3 pls.
- 1969. Tertiary ostracoda from the Isle of Wight and Barton, Hampshire, England. Part IV. *Ibid.* **12**, 149-170, 4 pls.
- 1970. Tertiary ostracoda from the Isle of Wight and Barton, Hampshire, England. Part V. *Ibid.* **13**, 13-29, 3 pls.
- 1971a. Tertiary ostracoda from the Isle of Wight and Barton, Hampshire, England. Part VI. *Ibid.* 207-221, 3 pls.
- 1971b. Tertiary ostracoda from the Isle of Wight and Barton, Hampshire, England. Part VII. *Ibid.* **14**, 147-156, 2 pls.
- 1971c. The stratigraphical distribution and palaeoecological significance of the Ostracoda from the Lower Tertiary Beds of the Hampshire Basin, England. *Bull. Cent. Rech. Pau—S.N.P.A.* **5**, suppl., 545-557.
- HOWE, H. V. 1971. Ecology of American torose Cytherideidae. *Ibid.* 349-359, 1 pl.
- HULINGS, N. C. and PURI, H. S. 1964. The ecology of shallow water ostracods of the West Coast of Florida. *Publ. Staz. zool. Napoli.* **33**, suppl., 308-344.
- JONES, T. R. 1856. Notes on the Entomostraca of the Headon and Osborne Series. In FORBES, E. 1856. On the Tertiary Fluvio-marine Formation of the Isle of Wight. *Mem. Geol. Surv. G.B.*, p. 157.
- 1857. A monograph of the Tertiary Entomostraca. *Palaeontogr. Soc. [Monogr.]*, 68 pp., 6 pls.
- and SHERBORN, C. D. 1889. A supplemental monograph of the Tertiary Entomostraca of England. *Ibid.* 55 pp., 3 pls.
- KAESLER, R. L. 1966. Quantitative re-evaluation of ecology and distribution of Recent Foraminifera and Ostracoda of Todos Santos Bay, Baja California, Mexico. *Paleont. Contr. Univ. Kansas.* **10**, 1-50.
- KAUFMANN, A. 1900. Cypriden und Darwinuliden der Schweiz. *Revue Suisse Zool.* **8**, 209-423, pls. 15-31.
- KEEN, M. C. 1968. Ostracodes de l'Éocène supérieur et l'Oligocène inférieur dans les Bassins de Paris, du Hampshire et de la Belgique, et leur contribution à l'échelle stratigraphique. In Colloque sur l'Éocène, Paris 1968, 1, *Mem. Bur. Rech. geol. min.* no. 58, 137-145.
- 1971. A palaeoecological study of the ostracod *Hemicyprideis montosa* (Jones and Sherborn) from the Sannoisian of North-West Europe. *Bull. Cent. Rech. Pau—S.N.P.A.* **5**, suppl., 523-543, 2 pls.
- 1972a. The Sannoisian and some other Upper Palaeogene Ostracoda from north-west Europe. *Palaeontology*, **15**, 267-325, pls. 45-56.
- 1972b. Mid-Tertiary Cytherettinae of north-west Europe. *Bull. Br. Mus. nat. Hist. (Geol.)*, **21**, 261-349, 23 pls.
- 1973a. On *Haplocytheridea debilis* (Jones). *Stereo-Atlas Ostr. shells*, **1**, 181-188.
- 1973b. On *Haplocytheridea mantelli* Keen sp. nov. *Ibid.* 189-192.
- 1975. The palaeobiology of some Upper Palaeogene freshwater ostracodes. *Bull. Am. Paleont.* **65**, 271-283.
- KEIJ, A. J. 1957. Eocene and Oligocene Ostracoda of Belgium. *Mem. Inst. R. Sci. nat. Belg.* no. 136, 210 pp., 23 pls.
- KILENYI, T. I. 1969. The problems of ostracod ecology in the Thames Estuary. In NEALE, J. W. (ed) *The taxonomy, morphology, and ecology of Recent Ostracoda*. Oliver and Boyd, Edinburgh, 251-267.
- 1972. Transient and balanced genetic poly-morphism as an explanation of variable nodding in the ostracode *Cyprideis torosa*. *Micropaleontology*, **18**, 47-64, pl. 1.
- KOLLMANN, K. 1960. Cytherideinae and Schulerideinae n. subfam. (Ostracoda) aus dem Neogen des ostlichen Oesterreich. *Mitt. geol. Ges. Wien*, **51**, 89-195, 21 pls.
- KORNICKER, L. S. 1965. Ecology of Ostracoda in the north-western part of the Great Bahama Bank. *Publ. Staz. zool. Napoli*, **33**, suppl., 345-360.

- LADD, H. S., HEDGPETH, J. W., and POST, R. 1957. Environment and Facies of Existing Bays on the Central Texas Coast. In (LADD, H. S.), *Mem. geol. Soc. Am.* **67** (2), 599–640.
- MALZ, H. 1973. Ostracoden aus dem Sannois und jungeren Schichten des Mainzer Beckens, 3. Ehemalige 'Cytheridea'—Arten und—Verwante. *Notissbl. Hess. L.-Amt. Bodenforsch.* **101**, 188–201, pls. 19–22.
- and MOAYEDPOUR, E. 1973. Miozane Susswasser—Ostracoden aus der Rhon. *Senckenberg. leth.* **54**, 281–309, 5 pls.
- MANDELSTAM, M. I. 1947. Ostracods from the Jurassic deposits of the Mangychlak Peninsula. In *Microfauna of the petroleum-bearing deposits of the Caucasus, Emba, and central Asia*, VNIGRI, 239–262, 2 pls. [In Russian.]
- MOORE, R. C. (ed.). 1961. *Treatise on Invertebrate Paleontology*, Part Q. Arthropoda 3. Crustacea, Ostracoda. Geol. Soc. Am. and Univ. Kansas Press, 442 pp.
- MOOS, B. 1970. Die Ostracoden-Fauna des Unteroligozans von Brandhurst bei Bunde (Bl. Herford-West, 3817), III. Schulerideinae MANDELSTAM 1959 und Cytherideinae Sars 1925. *Geol. Jb.* **88**, 289–320, 5 pls.
- MULLER, G. W. 1894. Ostracoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. *Fauna u Flora Neapel*, **21**, 403 pp., 40 pls.
- MURRAY, J. W. and WRIGHT, C. A. 1974. Palaeogene Foraminiferida and palaeoecology, Hampshire and Paris Basins and the English Channel. *Spec. Pap. Palaeont.* **14**, 129 pp., 20 pls.
- PURI, H. S. 1957. Notes on the ostracode subfamily Cytherideinae PURI 1952. *J. Acad. Sc. Washington*, **47**, 305–308.
- 1968. Ecologic distribution of Recent Ostracoda. In Proc. Symp. Crustacea, pt. 1, *Mar. biol. Ass. India* (1966), 457–495.
- REYMENT, R. A. and BRANNSTROM, B. 1963. Certain aspects of the physiology of *Cypridopsis* (Ostracoda, Crustacea). *Stockh. Contr. Geol.* **9**, 208–242.
- SANDBERG, P. A. 1964. The ostracod genus *Cyprideis* in the Americas. *Ibid.* **12**, 178, pl. 23.
- SARS, G. O. 1866. Oversigt af Norges marine Ostracoder. *Forh. VidenskSelsk. krist.* **7**, 1–131.
- 1925. An account of the Crustacea of Norway, 9. Ostracoda (1922–1928). *Bergen Mus.* **9**, 277 pp., 119 pls.
- SWAIN, F. M. 1955. Ostracoda of San Antonio Bay, Texas. *J. Paleont.* **29**, 561–646.
- SWARTZ, F. M. and SWAIN, F. M. 1946. Ostracoda from the Upper Jurassic Cotton Valley group of Louisiana and Arkansas. *J. Paleont.* **20**, 362–373, pls. 52–53.
- TRIEBEL, E. 1963. Ostracoden aus dem Sannois und jungeren Schichten des Mainzer Beckens: 1, Cyprididae. *Senckenberg. leth.* **44**, 157–207, 12 pls.
- VAN HARTEN, D. 1975. Size and environmental salinity in the modern euryhaline ostracod *Cyprideis torosa* (Jones, 1850), a biometrical study. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **17**, 35–48.
- VELLA, P. 1969. Correlation of base of Middle Headon Beds between Whitecliff Bay and Colwell Bay, Isle of Wight. *Geol. Mag.* **106**, 606–608.
- VESPER, B. 1972a. Zum Problem der Buckelbildung bei *Cyprideis torosa* (Jones, 1850) (Crustacea, Ostracoda, Cytheridae). *Mitt. Hamburg. Zool. Mus. Inst.* **68**, 79–94.
- 1972b. Zur Morphologie und Okologie von *Cyprideis torosa* (Jones, 1850) (Crustacea, Ostracoda, Cytheridae) unter besonderer Berücksichtigung seiner Biometrie. *Ibid.* 21–77.
- WAGNER, C. W. 1957. Sur les Ostracodes du Quaternaire Recent des Pays-Bas et leur utilisation dans l'étude géologique des depots Holocenes. *Diss. Univ. Paris*, 259 pp.
- WHATLEY, R. C. and KAYE, P. 1971. The palaeoecology of Eemian (Last Interglacial) Ostracoda from Selsey, Sussex. *Bull. Cent. Rech. Pau—S.N.P.A.* **5**, suppl., 311–330.

M. C. KEEN

Department of Geology
The University
Glasgow, G12 8QQ

Typescript received 27 February 1976

Revised typescript received 11 June 1976

APPENDIX

Details of sampling horizons for Headon Hill (HH) (SZ 305 860) and Whitecliff Bay (WB) (SZ 642 863) are given in text-fig. 1. Other samples mentioned are: from Headon Hill, HHCP2, *Cyrena pulchra* Bed sample no. 2 (see text-fig. 5); Base of UB, freshwater clay immediately below the Venus Bed; Base V.B., V.B. 18, Mid V.B., Top V.B., samples through the Venus Bed; NHH 1-4, samples from the horizon of HH48 collected in more detail. CB is Colwell Bay (SZ 327 878-330 890) 1 and 2 from the Oyster Bed, 4-6 from a blue sandy clay with shells 60-200 cm above the Oyster Bed, 12 a thin buff limestone in the Upper Headon Beds near Cliff End; HHL is the Howe Ledge Limestone of Colwell Bay; MF is Milford (SZ 278 917), 1 and 2 from the *Unio* Bed, 3 and 4 from the Middle Headon Beds; BC is Bouldnor Cliff (SZ 401 920), 3 topmost Bembridge Limestone, 570 cm above the limestone, 8, a further 120 cm higher; BR is Brockenhurst (SU 324 036), 1 and 3 from the Middle Headon Beds; Thorness Bay (SZ 464 945).